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Reef fish demographics on Louisiana artificial reefs : the effects of reef size on biomass distribution and foraging dynamics

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REEF FISH DEMOGRAPHICS ON LOUISIANA ARTIFICIAL REEFS:
THE EFFECTS OF REEF SIZE ON BIOMASS DISTRIBUTION AND
FORAGING DYNAMICS

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Oceanography and Coastal Sciences

by

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May 2013

DEDICATION

To Braxton, who has come so far, thus proving he can go anywhere.

To my grandparents, Stella and Joe, who taught me how to dream, and to Melissa,
who never had the chance.

And to all the Posdas, who help me to remember that I like fish, but that's ok.

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ABSTRACT

Understanding the role that habitat plays in the life history of reef-associated fishes is particularly significant given the dramatic increase in the number of artificial reefs deployed in coastal ecosystems over the past 50 years. In the Gulf of Mexico, the oil and gas industry has added a significant amount of structure to the Louisiana continental shelf, creating the largest *de facto* artificial reef deployment area in the world. Noting their usefulness as fish habitat, the Louisiana Artificial Reef Program was established to convert decommissioned platforms into artificial reefs. However, very little quantitative information exists on how these habitats affect the associated fish assemblage. The two objectives of this study were to examine high-resolution spatial and temporal distribution around two standing and two toppled platforms, and to examine the trophic ecology of common reef-associated fishes, such as red snapper (*Lutjanus campechanus*). Spatial distribution of fish biomass was examined using a multifrequency hydroacoustic approach to examine the extent of the area of influence around the two habitats and to examine diel changes in distribution. Standing platforms supported roughly two times higher biomass than toppled platforms, particularly in the upper water column at close ranges to the structures. Diel periodicity was evident, with higher biomass in the upper water column during the night and higher biomass in the lower water column during daylight hours. Diel periodicity was dependent on habitat and distance from the reef, breaking down at close range to standing platforms, likely a result of the light field emitted by working platforms. Trophic ecology was assessed with a combination of gut content and stable isotope analyses to examine both prey

and sources of basal resources to the reef habitats. Results indicate that red snapper are opportunistic feeders, and that artificial reef structures do not provide a unique set of prey items, indicating that prey and basal resources are consistently sourced from the surrounding water column and soft bottom sediments. Additionally, no evidence of an area of prey depletion (feeding halo) was found around the two habitats, further indicating that prey is derived opportunistically from areas surrounding the reef structures.

GENERAL INTRODUCTION

Of particular importance to reef-associated fishes is the habitat with which they associate, as habitat can affect all aspects of life history. Habitat, and the resources it provides, can profoundly affect spawning, feeding, growth, and mortality, and understanding how a particular habitat affects these various aspects of life history is important to understanding the role of habitat in the marine environment. Furthermore, the effects of adding structure in the form of artificial reefs, and the function these structures serve to the associated reef fish assemblage is an important part of deciphering whether they can be used as a fisheries management tool (Cowan et al. 2011).

The northern Gulf of Mexico (GOM) is home to approximately 3500 oil and gas platforms, creating the largest *de facto* artificial reef deployment area in the world. The first oil platform in the GOM was installed in 1947, and since that time over 5500 have been constructed; subsequently, over 4000 have now been decommissioned and removed (Dauterive, 2000; BOEM, personal communication). While the main function of these structures is the production of oil and gas, the secondary effect is an increase in the amount of hard substrate present in the GOM, the majority of which is in areas that lack hard bottom substrate (Scarborough-Bull et al. 2008). This addition of hard substrate provides additional habitat for the attachment of many sessile invertebrates and macroalgae (Scarborough-Bull et al. 2008), which in turn supports a diverse community, differing greatly from that found on the surrounding soft-bottom habitats. In this sense, it is estimated that the presence of oil and gas platforms has increased the overall biomass in the GOM at

least for nonharvested species of fishes, invertebrates, and macroalgae (Scarborough-Bull et al. 2008). It was quickly realized that these large structures also attracted fishes, and supported a healthy community of reef-associated fishes, providing easy access for recreational and commercial fishers, as well as SCUBA divers. The accessibility of oil and gas platforms for fishing and other recreation led to the establishment of the Rigs-to-Reefs Program in the GOM (Kaiser, 2006). Bureau of Ocean Energy Management (BOEM) rules state that a platform must be decommissioned within one year of the termination of a lease in the GOM (Dauterive 2000; Kaiser 2006). BOEM allows the transfer of a lease to a state sponsored program that then becomes responsible for the maintenance of the structure as an artificial reef.

Artificial reef programs are in place throughout the United States. In most cases, the reef programs are monitored by state government agencies, or not at all. Materials designated for reef building may be derived commercially, such as reef balls, or from “materials of convenience”, which can include anything from sunken vessels to subway cars. In Louisiana, the artificial reef program relies almost exclusively on material from decommissioned oil and gas platforms (Kaiser, 2006). There had been a push for use of decommissioned platforms to be turned into artificial reefs, due to the economic benefits to the energy companies involved, especially for large or complex rigs, and those in deep water, which are more expensive to remove (Kaiser, 2006). Therefore, a number of artificial reef planning areas have been set up, based on a set of criteria determined by BOEM (Dauterive,

2000). To date, over 300 structures have been turned into artificial reefs in nine planning areas that exist in the GOM (Wilson and Van Sickle 1987).

Despite the support for the rigs-to-reefs program, little is known about how decommissioned platforms function as fish habitat. Extensive work has been conducted monitoring colonization, abundance, and distribution of reef fishes on small, coastal artificial reefs around the world (Bohnsack 1989; Bohnsack et al. 1997; Lindberg 1997; Bortone 1998; see Fisheries v. 22, 1997 for a review), however there is a paucity of quantitative information on the function of large artificial reefs, such as standing and toppled oil and gas platforms. This is surprising given the valuable commercial and recreational fishery that they support in the Gulf of Mexico. Furthermore, examination of small artificial reefs has revealed that zones of prey depletion can develop around the reef, creating “feeding halos” necessitating longer, more energetically costly foraging migrations (Lindberg et al. 1990; Lindberg et al. 2006). These feeding halos have been shown to be dependent on reef size and proximity of other reefs (Shipley and Cowan 2010; Campbell et al. 2011), but have not been empirically examined at the scale of large reefs such as oil and gas platforms.

This project sought to address, in part, the specific roles of standing and toppled oil and gas platforms in two specific aspects of reef fish life history. The first part seeks to address how reef fish biomass associates with standing and toppled platforms with high spatial and temporal resolution. This is accomplished through a mobile hydroacoustic approach. Hydroacoustics have proven to be effective at addressing spatial distribution of reef-associated fishes in the Gulf of

Mexico (Stanley and Wilson 1996, 1997, 1998, 2000, 2003; Wilson et al. 2003; Wilson et al. 2006; Boswell et al. 2010), and can gather information on much finer spatial scales than traditional sampling gear. Furthermore, a large amount of data can be collected in a relatively noninvasive manner with less effort than traditional sampling methods, allowing for high temporal resolution of data collection. Chapter 1 examines the spatial distribution of reef fish biomass around standing and toppled platforms. One of the key limitations of hydroacoustics is the lack of information on species, and so I have utilized a multifrequency approach to broadly classify groups of scatterers, and to further understand how habitat differentially affects different species, or classes of organisms. Chapter 2 examines the diel movement patterns of reef-associated fishes around standing and toppled platforms. By continuously sampling the water column around the reef structures for 48 hours, I was able to examine movement patterns with high spatial and temporal resolution to examine differences in diel periodicity between the two types of artificial reefs.

The second half of my dissertation examines the trophic dynamics of reef-associated fishes, specifically red snapper (*Lutjanus campechanus*), through the incorporation of gut content and stable isotope analyses. Chapter 3 examines differences in trophic dynamics of red snapper among three habitats, including standing and toppled oil and gas platforms, and natural shelf edge bank reefs. Chapter 4 seeks to determine whether prey resources are locally depleted around standing and toppled platforms, creating a feeding halo. Here, I examined two common demersal fish species, red snapper and rock sea bass (*Centropristis philadelphica*) to examine trophic ecology between habitat types, among seasons,

and with distance from the artificial reef structures. Through the use of hydroacoustics to examine spatial distribution on a large scale, and diet analyses to examine prey distribution on a smaller scale, my goal was to gain a better understanding of how large artificial reefs function as habitat in the Gulf of Mexico.

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CHAPTER 1: SPATIAL DISTRIBUTION OF REEF-ASSOCIATED FISHES AROUND STANDING AND TOPPLED OIL AND GAS PLATFORMS IN THE NORTHERN GULF OF MEXICO

Introduction

The northern Gulf of Mexico (GOM) is home to approximately 3000 oil and gas platforms, creating the largest *de facto* artificial reef deployment area in the world. The first oil platform in the GOM was installed in 1947, and since that time over 6500 have been constructed; subsequently, nearly 4000 have now been decommissioned and removed (Dauterive, 2000; BOEM, personal communication). While the main function of these structures is the production of oil and gas, one secondary effect is an increase in the amount of hard substrate present in the GOM, the majority of which is in areas that lack hard bottom substrate (Scarborough-Bull et al. 2008).

The Bureau of Ocean Energy Management (BOEM) requires that a platform must be decommissioned within one year of the termination of a lease in the GOM (Dauterive 2000; Kaiser 2006), and subsequently allows the transfer of a lease to a state sponsored program that then becomes responsible for the maintenance of the structure as an artificial reef. Artificial reef programs are in place throughout the United States, and in most cases are monitored by state government agencies. Materials designated for reef building may be derived commercially, such as Reef Balls™, or from “materials of convenience”, which can include anything from sunken vessels to subway cars. In Louisiana, the artificial reef program relies almost exclusively on material from decommissioned oil and gas platforms (Kaiser, 2006). There had been a push for use of decommissioned platforms to be turned into

artificial reefs, due to the economic benefits to the oil companies involved, especially for large or complex platforms, and those in deep water, which are more expensive to remove (Kaiser, 2006). Therefore, a number of artificial reef planning areas have been set up, based on a set of criteria determined by BOEM (Dauterive, 2000). To date, over 400 structures have been converted to artificial reefs, > 300 of those have been placed in one nine planning areas that exist off Louisiana (Wilson and Van Sickle 1987, and subsequent reauthorizations).

Despite the extensive artificial reef program in Louisiana, very little information exists on how decommissioned platforms affect the associated fish community. In general, artificial reefs are well known as aggregators of reef-associated fishes (Hastings et al. 1976; Bohnsack 1989; Bohnsack et al. 1997; Grossman et al. 1997; Lindberg 1997; Bortone 1998; Stanley and Wilson 1996, 1997, 1998, 2000), and oil and gas platforms are known to support a high fish biomass in the GOM (Stanley and Wilson 1996, 1997, 1998, 2000; Boswell et al 2010). The unique feature of standing oil and gas platforms as artificial reefs is that they provide structure throughout the water column, extending into the photic zone and providing structure that attracts pelagic fishes such as blue runner (*Caranx crysos*), spadefish (*Chaetodipterus faber*), and large pelagic fishes such as amberjack (*Seriola dumerili*), barracuda (*Sphyraena barracuda*), and many species of sharks (Hastings et al. 1976; Stanley and Wilson 1997; Brown et al. 2010). BOEM requires that decommissioned platforms to be converted to artificial reefs be severed 30 m below the surface so as not to hinder navigation (Dauterive 2000; Kaiser 2006). Because toppled platforms are missing the top 30 m of structure that extends into

the photic zone, the associated fish assemblage may be different from that associated with standing oil and gas platforms. However, few studies have examined this relationship (but see Wilson et al. 2003; 2006).

One important step in deciphering the role of standing and toppled oil and gas platforms to the ecology of reef-associated fishes is to understand their spatial distribution around the structures. The spatial distribution of fishes associating with artificial reefs has been examined in numerous areas including the North Sea (Lokkeborg et al. 2002; Sodal et al. 2002), the Mediterranean Sea (Fabi and Sala, 2002; Sala et al. 2002), Africa (Gerlotto et al. 1989), South America (dos Santos et al. 2010), and in the GOM (Stanley and Wilson 1996, 1997, 1998, 2000; Boswell et al. 2010). These studies have all observed a consistent pattern of exponential decline in both fish biomass and abundance with distance from the reef structure. The result is an area of concentrated fish biomass near the structure, or “zone of influence”, which decreases with distance until some background level of biomass is reached.

Previous reports on the spatial extent of the zone of influence have varied, reporting peaks in abundance ranging from 10 m from the reef structure (Stanley and Wilson 1998) to 300 m from the reef structure (Lokkeborg et al. 2002), with the majority of studies reporting the range to be between 50 and 100 m regardless of reef size (Gerlotto et al. 1989; Stanley and Wilson 1996, 1997, 2000; Fabi and Sala, 2002; Sodal et al. 2002; Sala et al. 2002; dos Santos et al. 2010; Boswell et al. 2010). Examination of small, concrete patch reefs in Brazil revealed significantly lower abundance of fish at 50 m from the reef structure based on visual and gill net

surveys (dos Santos et al. 2010). Similarly, Fabi and Sala (2002) reported significantly lower fish biomass 80 m outside a patch reef in the Adriatic Sea. Gerlotto et al. (1989) first reported the “platform” effect on fish abundance, observing an area of high abundance within approximately 150 m of an oil and gas platform in Camaroon. Observations of oil and gas platforms in the North Sea have revealed conflicting results, where Lokkeborg et al. (2002) observed a higher catch totals in gill net sets within 200 m of the platform during May sampling, and at 150 – 300 m during September sampling, when catches were dominated by cod (*Gadus morhua*). At the same platforms, Soldal et al. (2002) observed no effect of distance from the platform structure during their surveys. It should be noted though that in each of the North Sea studies sampling was restricted to a distance of 50 – 100 m from the platform for safe operations. In the GOM, Stanley and Wilson (1996, 1997, 1998, 2001) reported higher densities within 10 – 20 m of oil and gas platforms, while Boswell et al. (2010) reported similar findings at a shallow large artificial reef complex near the coast.

Incorporating the near field region around artificial reefs is crucial to understanding their function as habitat, as there is high nekton abundance and increased variability within the first 100 m of the reef structure. Hydroacoustics is a useful tool to assess the spatial distribution of the nekton around large artificial reefs, as it provides a noninvasive technique to acquire data over large areas with higher spatial resolution than traditional fishing gears (Stanley and Wilson 1997, 1998, 2001; Benoit-Bird et al. 2001; Simmonds and MacLennan 2005; Boswell et al. 2010). Hydroacoustics have been used to effectively map the spatial associations of

fish biomass associated with large artificial reef structures in the North Sea (Soldal et al. 2002), the Mediterranean Sea (Fabi et al 2002) and the GOM (Stanley and Wilson 1996, 1997, 1998, 2000; Boswell et al. 2010). The goal of this chapter was to map the spatial distribution of reef-associated fishes around both standing and toppled oil and gas platforms, and to contrast the spatial and temporal pattern in the zone of influence between the two platform configurations.

Methods and Materials

Two standing oil and gas platforms (hereafter standing) and two decommissioned and toppled oil and gas platforms (hereafter toppled) were examined in this study. Toppled platforms have the surface deck structures and infrastructures removed, are cut approximately 30 m below the surface, and the remaining structure is placed on the seafloor adjacent to the platform base (Kaiser 2006). Study sites were located in the Eugene Island (EI) block of the Louisiana coast in the northern Gulf of Mexico (GOM) (Figure 1.1). Standing platforms included EI 325 and EI 346, and toppled platforms included EI 322 and EI 324. Sampling was conducted quarterly from November 2008 through August 2010 to examine both habitat and seasonal effects on reef fish distribution. EI 322, 324, and 325 are located in approximately 70 m water depth, and EI 346 is located in approximately 85 m water depth.

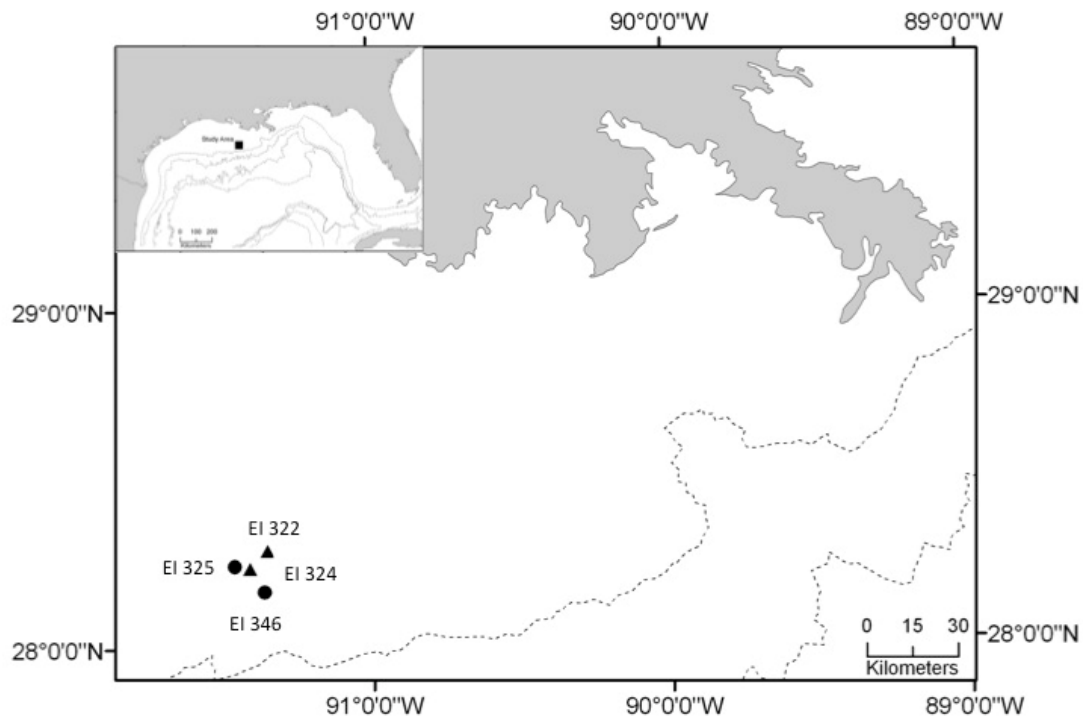


Figure 1.1: Sampling locations for acoustic data collection in the Eugene Island (EI) block of the northern Gulf of Mexico. Sites include two standing (circles) and two toppled (triangles) oil and gas platforms.

Environmental data were collected at each site during each sampling trip with a Sea-Bird SBE 25 CTD profiler. Eight CTD casts were conducted in a transect running north to south at each site at distances of 1.5, 1.0, 0.5, and 0.25 km both north and south of the platform structure. Water quality parameters collected include conductivity, temperature, pressure, depth, salinity, dissolved oxygen and optical backscatter. Values of temperature, salinity, and dissolved oxygen were examined at each habitat and season for comparison with fish distribution.

Acoustic backscatter data were collected using a BioSonics echosounder equipped with three downward-looking split-beam transducers (70, 120, and 200

kHz), calibrated by the standard sphere method (Foote et al. 1987). Data were collected at a threshold of -100dB, with a pulse duration of 0.4ms. The vessel was equipped with a bulbous bow and kort nozzle propellers, which were designed to provide a smoother ride and help reduce the level of acoustic background noise produced by the ship. Surveys were conducted at an average speed of 2 m s⁻¹ and each transect was approximately 2 km in length, with the reef structure at the midpoint. Ten transects were completed at each site, conducted in a star-shaped pattern, with each transect offset 18° from the previous line (Figure 1.2). Transducers were mounted on a pivoting boom that was lowered when on site, extending approximately 2 m depth below the surface to avoid bubbles entrained in the ships wake.

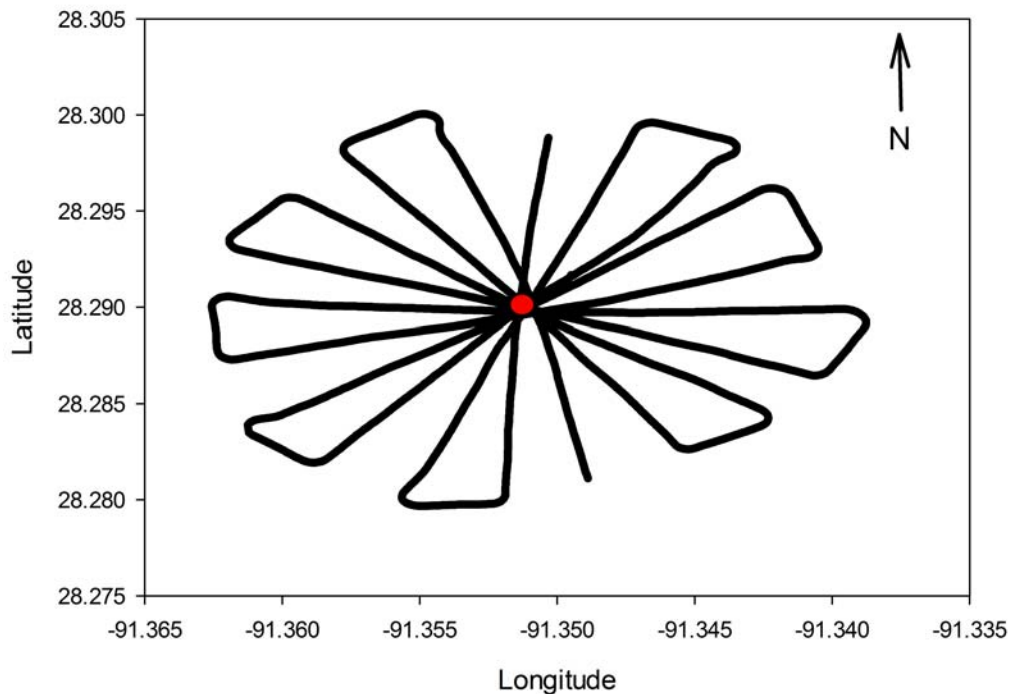


Figure 1.2: Approximation of cruise track used during acoustic sampling. Red circle represents geographic center point of reef structure.

Acoustic backscatter data were post-processed using Echoview v. 5.3 (Myriax Pty. Ltd., Hobart, Tasmania, Australia) to obtain values of mean volume backscatter (MVBS, S_v , dB). Analysis thresholds were set in Echoview for S_v , and calibration settings were applied to compensate for the effects temperature and salinity on speed of sound. All echograms were visually inspected to exclude regions of bad data (i.e., signal loss, noise). Data within 2 m of the transducer face was excluded to account for surface noise, transducer ringdown and near field effects. A bottom detection algorithm with a 0.5m backstep (Ona and Mitson 1996) was applied to exclude the seafloor and reef structures from the analysis and then manually edited as needed. Mean volume backscattering strength (MVBS; S_v , dB) data, integrated at 10 m depth by 10 m distance bin, were exported from Echoview and used for analysis of spatial and temporal distribution of the fish community around platform habitats. MVBS represents the total integrated energy of targets in the water column and the intensity of backscattered energy is understood to be proportional to the biomass of nekton in the water column (Simmonds and MacLennan 2005).

Acoustic targets were classified into representative groups (i.e, fish, zooplankton) within the echograms in Echoview through the process of dB differencing, using the 120 kHz and 70 kHz transducers. Swim-bladdered fish are known to have decreasing values of S_v with increasing frequency (Korneilussen and Ona 2002; Korneilussen et al. 2009; De Robertis et al. 2010), while fish lacking swim bladders are relatively frequency independent at lower frequencies, with a sharp increase at 200 kHz (Korneilussen and Ona 2002; Korneilussen et al. 2009). For this reason, the 70 kHz and 120 kHz frequencies are most appropriate for differentiating

between fish and zooplankton scatterers following Madureira et al (1993), Korneilussen and Ona (2002), Mosteiro et al. (2004), Korneilussen et al. (2009) and De Robertis et al. (2010). First, 120 kHz and 70 kHz echograms were matched in time to assure that samples were temporally coincident. Following this, background noise and intermittent noise spikes were suppressed within in Echoview following methods described in De Robertis and Higginbotham (2007). Frequency response differencing was achieved by subtracting each sample at 70 kHz from the corresponding sample at 120 kHz (Figure 1.3). The resulting data were classified into two groups based on the relative frequency response where sample Sv_{120-70} ranging from -15 to 1, was labeled as swim-bladdered fish (Madureira et al. 1993; Korneilussen and Ona 2002; Mosteiro et al. 2004; Korneilussen et al. 2000; De Robertis et al. 2010) and sample Sv_{120-70} ranging from 3 to 25, was classified as zooplankton (Madureira et al. 1993; Korneilussen and Ona 2002; Korneilussen et al. 2000; De Robertis et al. 2010)(Figure 1.3).

Data Analysis

Environmental data were post-processed using SeaBird SBE Data Processing Software v 7.22.4 (Sea-Bird Electronics, Seattle, WA, USA). Mean values of temperature, salinity, and dissolved oxygen were compared with depth between habitats and among seasons with a multiple analysis of covariance (MANCOVA), using depth as a covariate (SAS v. 9.2, Cary, North Carolina, USA).

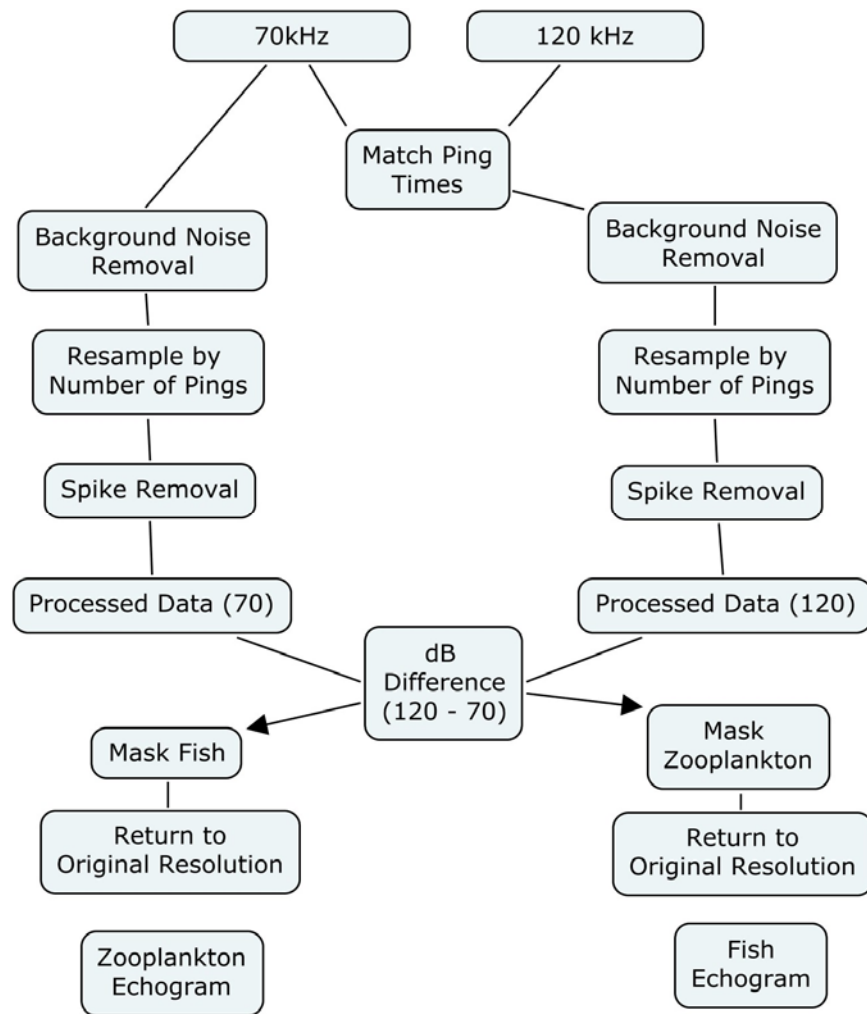


Figure 1.3: Schematic of the Echoview Data Flow used in processing of acoustic data.

Mean volume backscattering strength was linearized and compared between habitats, among seasons, and as a factor of depth and distance from the reef structure using a generalized linear mixed model (GLIMMIX, SAS v. 9.2, Cary, North Carolina, USA), with MVBS used as the dependent variable in the model. The geographic midpoint of each reef structure was determined, and distance was calculated for each data point from that geographic mean in SAS. Depth bins were further combined from 0 – 30 m, 30 – 60 m, and 60+ m for statistical analysis to

examine differences in the upper, middle and lower water column based on differences reported in Stanley and Wilson (1998). Two separate models were run to compare MVBS with habitat, season, depth and distance. The first modeled distance as a continuous covariate to the effects of habitat, season, and depth. The second model examined five discrete distances of 10, 50, 100, 200, and 500m, to more closely examine the changes in MVBS with distance. These distances were chosen based on preliminary observations of the data.

Acoustic Classification

Multiple frequency acoustic backscatter data was used to classify scatterers based upon their relative frequency response, following Korneilussen and Ona (2002) and Korneilussen et al. (2009). Echograms were processed by matching corresponding ping times in the 120 and 200 kHz echograms to the 70 kHz to assure consistency in time and space, applying background noise removal and spike filters (see De Robertis and Higginbottom 2007), to obtain cleaned, processed data for all three frequencies. Following the filtering approach, an XxY matrix convolution was applied to smooth sample data and reduce ping-to-ping variability. A 1 x 21 matrix, corresponding to 1 ping (X) by 21 samples (Y) was applied to smooth echograms in the vertical domain. A school detection algorithm was applied in Echoview in each frequency echogram, giving a maximum of three values for each region. Data were exported in region x cell format from each frequency, and combined in space and time to create one data set where each cell had three Sv

values as detected by each frequency. Relative frequency response was determined using the subtraction method to create ΔdB values using the following formula:

$$\Delta\text{db}_{i-j} = \text{Sv}_i - \text{Sv}_j$$

where Δdb_{i-j} is the value for each frequency, i , as compared to a reference frequency, j .

Classification was limited to include four broad classes of organisms, including large pelagic predators (LPP), schooling planktivores (SP), fish, and zooplankton scattering layer. The LPP group consists of larger piscivores without swimbladders, such as king mackerel (*Scomberomorus cavalla*) and sharks. Schooling planktivores are species such as blue runner, spadefish, and Bermuda chub (*Kyphosus sectatrix*) found in the upper water column, near the structure, in tightly packed schools. The “fish” and “zooplankton” classes are broad classifications encompassing the remaining majority of scatterers. Acoustic classification has mostly been used in high latitude regions, where species diversity is low, therefore enabling classification down to genus and in some cases species level (Korneilussen and Ona 2002; Korneilussen et al. 2009; De Robertis et al. 2010). In the GOM, acoustic classification is difficult due to the high number of species present (Stanley and Wilson 2003; Wilson et al. 2006; Boswell et al. 2010), and the lack of target strength information for most species, and has not been attempted in reef fish communities. For these reason, classification was limited to broad classes, and scatterers that could be identified through visual observation. Classification rules were based upon those established for similar species by Korneilussen and Ona (2002), Korneilussen et al. (2009), and De Robertis et al. (2010), and are listed

in Table 1.1. Detection of schooling planktivores was limited to regions near the structures, and depths < 50 m based upon the results of a tagging study examining spatial movements of blue runner reported by Brown et al. (2010), the most commonly observed SP at the study sites.

Spatial distribution of each acoustic class was statistically analyzed using a general additive model (GAM), a form of nonparametric regression. GAM models allow for modeling of nonparametric responses with multiple independent variables, and modeling data that is not normally distributed. Each acoustic class was modeled separately using a GAM to examine the relationship with depth and distance at each habitat. Models fit the linearized MVBS of each class to depth and distance at each habitat, using a spline smoothing of the independent variable. Separate models were fit for each habitat to examine the differences in the response of each acoustic class at each habitat. Following GAM models, a general linear model (GLM) was fit to MVBS of each acoustic class to determine if differences existed in the mean backscatter of each class between habitats and among seasons, with distance as a covariate. The GAM model was used to examine the relationship in space of each class to the structure, while the GLM was used to determine if there were differences in the amount of scattering of each class between habitats and among seasons. Both GAM and GLM models were performed in SAS (v. 9.2, Cary, North Carolina, USA).

Table 1.1: Classification rules applied to acoustic backscatter based on frequency response.

Classification	Δdb_{i-j}			Description	Constraints
	120 - 70	200 - 70	200 - 120		
Large Pelagic Predators	> 4	> 7	> 2	Sv increases with increasing frequency, peaked at 200 kHz	None
Schooling Piscivores	> 0	> 0	< 0	Sv increases from 70 to 120 kHz and decreases from 120 to 200 kHz	Depth < 50 m Distance < 200 m
Fish	< 0	$-2 < \Delta db_{120-70} < -5$	< 0	Weakly decreasing Sv with increasing frequency	None
Zooplankton	> 0	$> \Delta db_{120-70}$	> 0	Increasing Sv with increasing frequency	None

Results

A total of 8 cruises were completed during the course of the study. In 2009, transects were completed at all four sites in January, April, and July, and three of the sites were sampled in June 2009. In 2010, transects were completed in January, March, April, and July. No data were collected from fall samples due to a combination of weather and equipment issues. Therefore, seasonal comparisons are limited to winter, spring, and summer, only.

The water column at both habitats remained well mixed throughout much of the year, except in the summer when a distinct thermocline and halocline were present (Figure 1.4), characterized by warmer and lower salinity water in the surface layer down to approximately 30 m depth. Due to weather conditions and equipment issues, data in the fall are only available at standing platforms, and data in the winter are only available at toppled platforms. Results of the MANCOVA indicate that there were significant differences in temperature, salinity, and DO with the main effects of season, habitat, and the covariate, depth ($p < 0.0001$, MANCOVA, SAS). Higher order interactions of habitat x season and habitat x season x depth were not significant ($p > 0.05$). This disparity is likely due to the large data set, and differences with habitat are likely not biologically significant. More importantly, results of the CTD data indicate that DO never fell below $2 \text{ mg} \cdot \text{L}^{-1}$ in the study area (Figure 1.4), indicating that the study sites were not hypoxic at the time sampling was conducted.

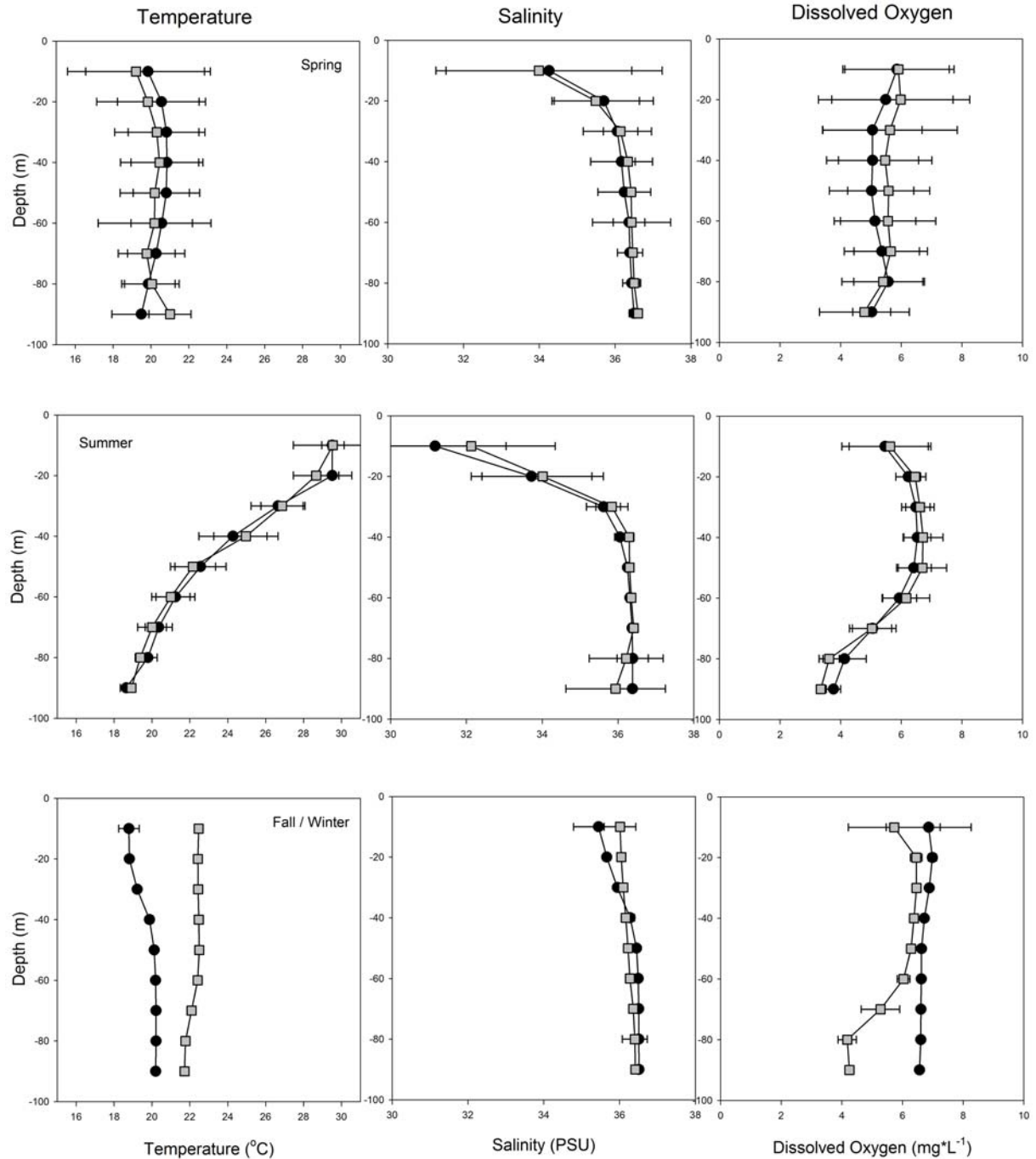


Figure 1.4: Results of CTD profiles at two habitats in the northern Gulf of Mexico. Data are combined among transects at each habitat. In all figures, black circles represent standing platforms and grey squares represent toppled platforms. Left column is temperature (°C), middle is salinity (PSU), and right is dissolved oxygen (mg·L⁻¹). Top row are spring samples, middle are summer samples and bottom are fall/winter. Fall and winter are combined in one panel because data are only available from standing platforms in the fall and from toppled platforms in the winter. Standard error bars are shown.

MVBS was highly variable throughout the study sites and study period. Results of the GLIMMIX model indicate significant differences in MVBS between habitats, among seasons, with depth, and with distance from the structures ($p < 0.0001$, GLIMMIX, SAS, Table 1.2). MVBS was highest within 20 m of the reef structure at both habitats (Figure 1.5), and all seasons (Figure 1.6), and declined rapidly with distance, reaching background levels between 80 and 150 m, varying with habitat and season (Figure 1.6). Combined over seasons, MVBS was more than two times higher at standing platforms within 50 m of the structure, while toppled platforms had significantly higher levels of background MVBS in the upper water column (Figure 1.5). MVBS was significantly higher in the summer at both habitats, particularly in the upper water column where MVBS was two times greater than the other seasons. In the lower water column, MVBS was similar between habitats, increasing between 0 and 50 m from the reef and decreasing again before reaching background levels at around 100 m (Figure 1.5). Background levels of MVBS remained consistent throughout the year.

LS means of MVBS were compared at five distinct distances, revealing significant differences among most pairwise comparisons ($p < 0.05$, GLIMMIX, SAS). Results of pairwise comparisons further indicate that MVBS is highly variable with depth, distance and season, but was consistently highest in the surface layer (< 30 m), except in the winter at toppled platforms when the lower water column had significantly higher MVBS (Figure 1.7). Despite high variability in the data, MVBS was more consistent at the 90 m depth interval between habitats and among seasons. Trends in the data are relatively consistent with distance from the

structures. MVBS was higher at the standing platforms at all distances in the upper and middle water column, and higher at toppled platforms in the lower water column at all distances (Figure 1.7). MVBS was highest in the summer at all distances in the upper and middle water column, and was higher in the lower water column at all distances in the winter (Figure 1.7).

Table 1.2: ANOVA table type III fixed effects from the GLIMMIX model comparing MVBS with habitat, season, depth, and distance. Significance was set at $\alpha = 0.05$ for all tests.

Source	df	F-value	p-value
Habitat	1	20.48	< 0.0001
Season	2	108.23	< 0.0001
Depth	2	235.57	< 0.0001
Distance	1	186.53	< 0.0001
Habitat x Season	2	6.12	0.0022
Habitat x Depth	4	16.77	< 0.0001
Habitat x Distance	1	65.46	< 0.0001
Habitat x Season x Depth	4	7.46	< 0.0001
Habitat x Depth x Distance	2	53.23	< 0.0001
Habitat x Season x Depth x Distance	4	9.23	< 0.0001

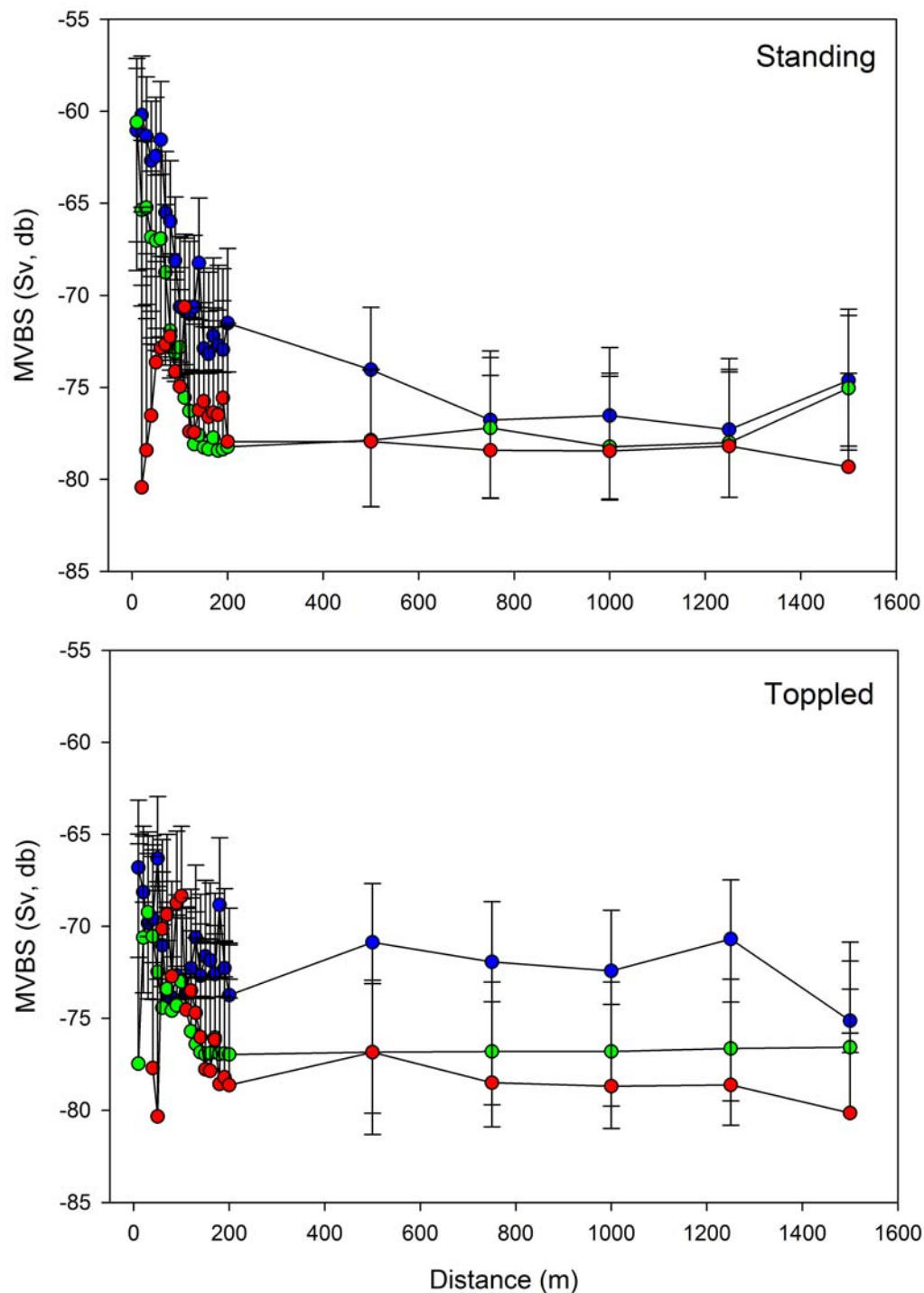


Figure 1.5: Mean volume backscatter (MVBS, Sv) of fish scatterers with distance from the reef structure at two habitats in the northern Gulf of Mexico. Top panel shows standing oil and gas platforms (circles) and lower panel shows toppled oil and gas platforms (squares). Blue symbols are upper water column (0 – 30 m), green symbols are middle water column (30 – 60 m), and red symbols are lower water column (> 60 m). Standard error bars are shown.

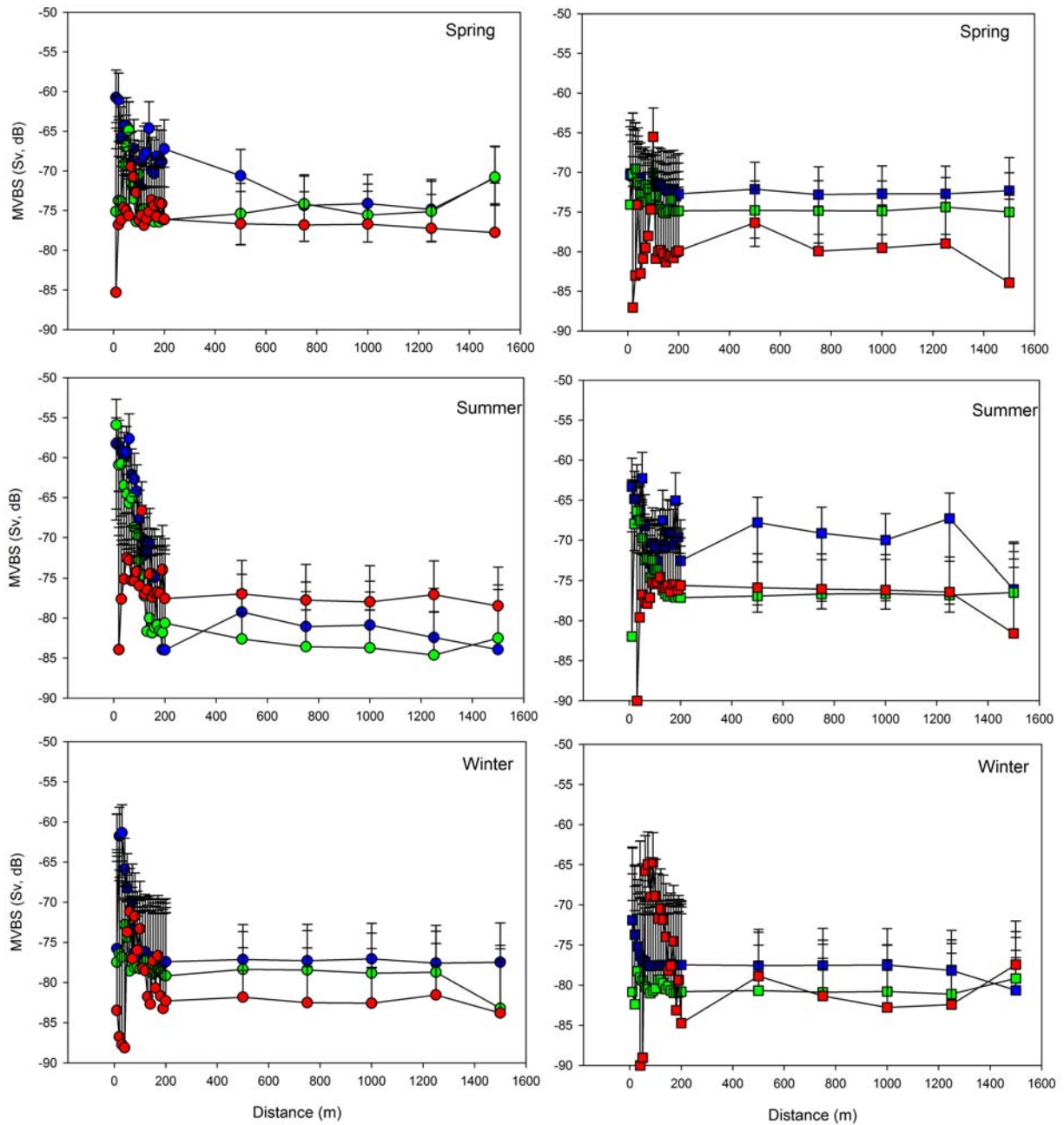


Figure 1.6: Mean volume backscatter (MVBS, Sv, dB) of fish scatterers by season and with distance from the reef structure at two habitats in the northern Gulf of Mexico. Left panel is standing oil and gas platforms (circle). Right panel is toppled oil and gas platforms (square). Blue symbols are upper water column (0 – 30 m), green symbols are middle water column (30 – 60 m), and red symbols are lower water column (> 60 m).

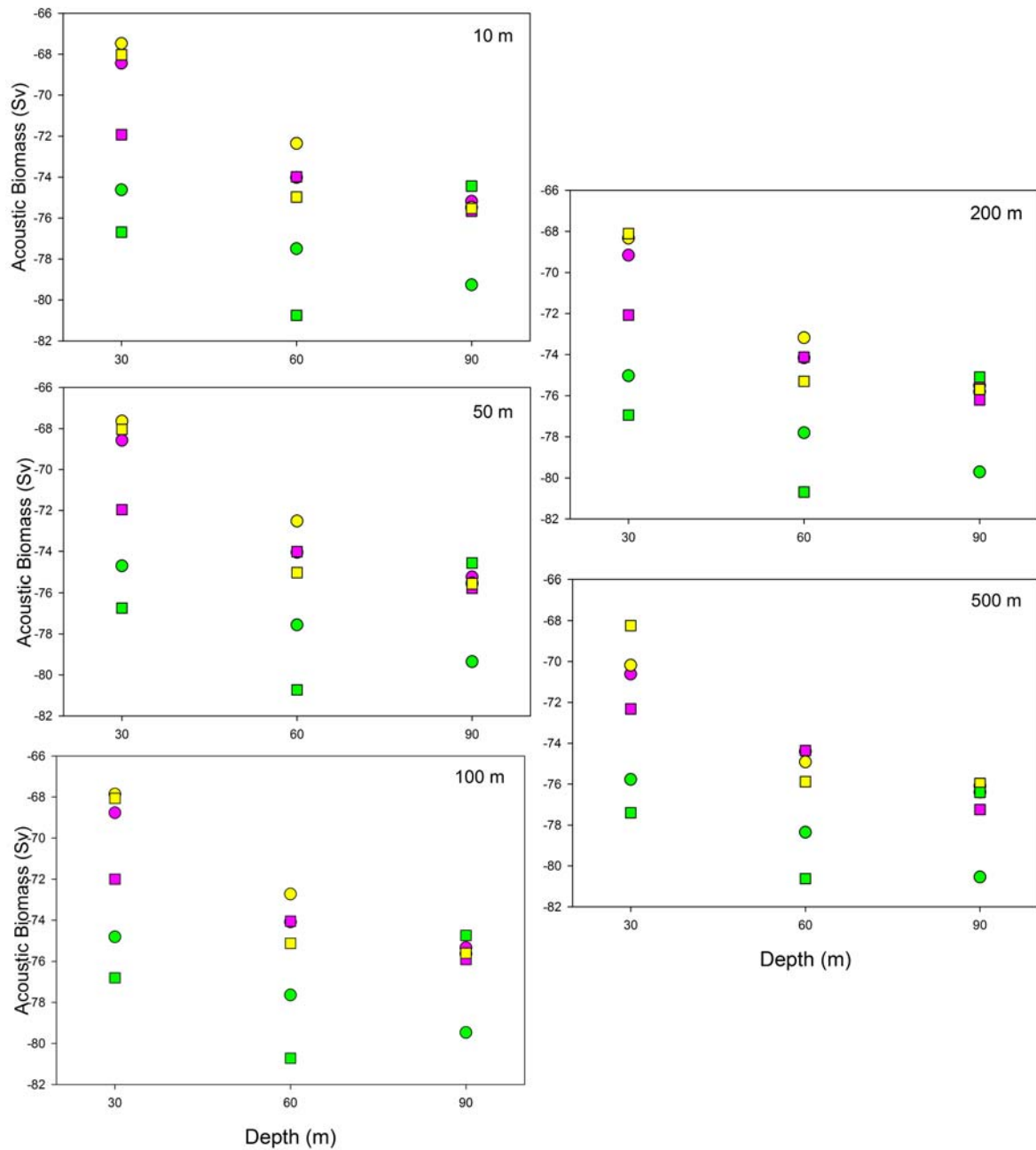


Figure 1.7: Results of LSmeans pairwise comparisons of MVBS for habitat x depth x season interactions at five discrete distances from structures: 10, 50, 100, 200, and 500 m. Circles represent standing platforms and squares represent toppled platforms. Pink represents spring samples, yellow represents summer samples and green represents winter samples.

Classifications worked well for the LPP class, which due to the lack of a swimbladder, had a very distinct response based on frequency response (Figure 1.8). Classification also worked well for the SP class, once the classification was constrained to areas with known targets. The SP class had a very distinct school shape, which was easily distinguishable in echograms compared to other fish scatterers (Figure 1.8). Classification for the fish and zooplankton schools was more challenging, largely stemming from the lack of target strength information and mixed species assemblage present, however they did separate out in the echograms (Figure 1.8).

All acoustic classes showed different responses to depth and distance based on the GAM models. The LPP class exhibited a significant response with both depth and distance ($p < 0.0001$, GAM). MVBS of LPP was higher in the upper water column at both habitats, decreasing at around 20 m depth at both standing and toppled platforms (Figure 1.9). At both habitats, MVBS increased again around 60 m depth. The response with distance was different between habitats, with standing platforms having higher biomass near the structures (< 200 m distance) and biomass peaking approximately 300 m from the toppled structures (Figure 1.9). At both habitats, MVBS remained increased again between 700 and 1000 m. Results of the GLM indicate that there were no differences in acoustics scatter of LPP between habitats ($p = 0.22$, GLM), but there were seasonal differences, with Tukey post-doc testing confirming higher biomass in summer ($p < 0.0001$, GLM) (Table 1.3). The fish class also exhibited a significant response with distance based on the GAM model ($p < 0.0001$, GAM). Response with depth differed between habitats, and was

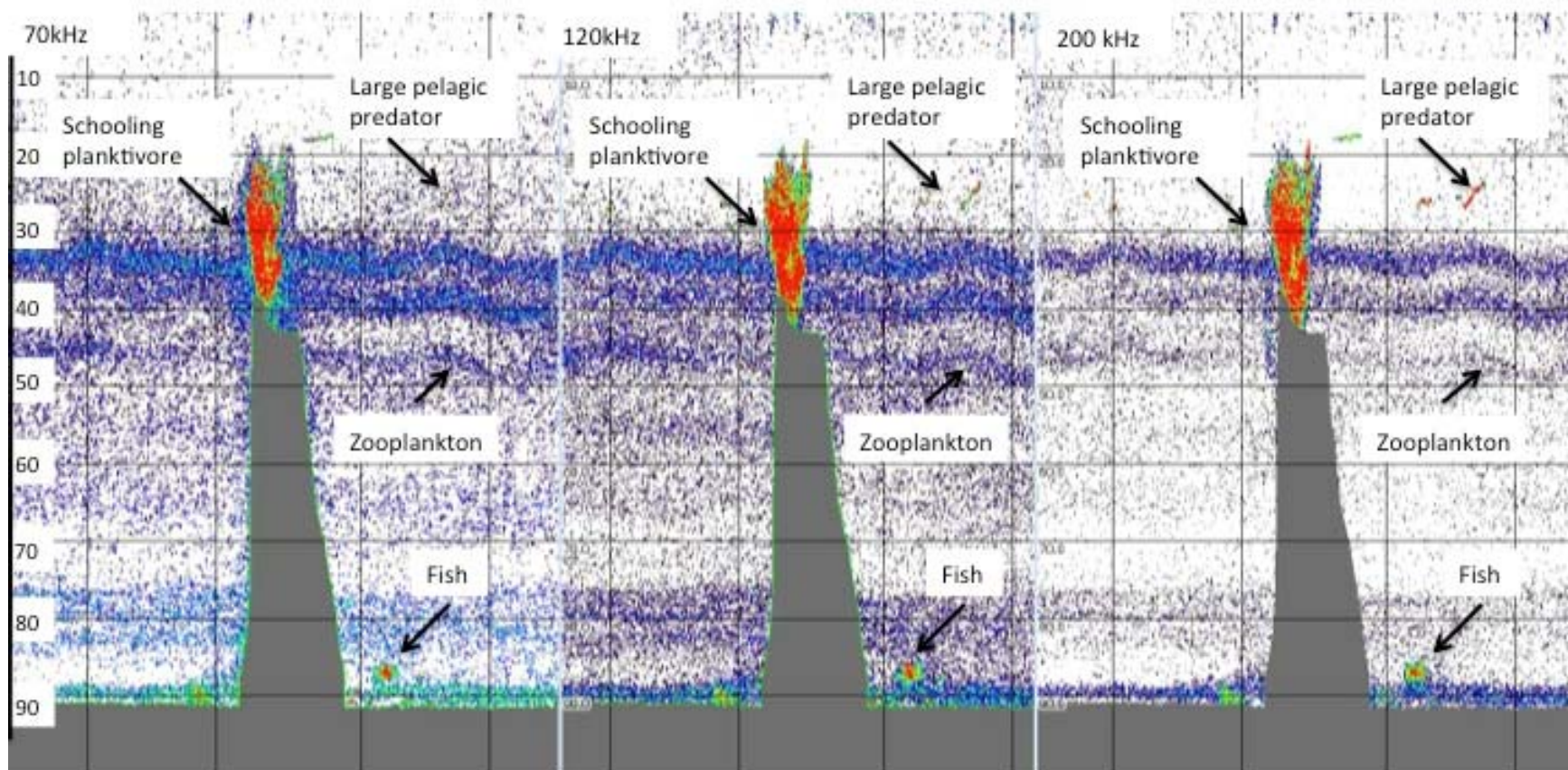


Figure 1.8: Example echogram showing four distinct classes of acoustic scatterers including large pelagic predators, schooling planktivores, fish, and zooplankton. The three different frequencies are shown, from left to right, 70, 120, and 200 kHz. Depth in meters is shown on the left. The grey area indicates the bottom and the platform structure.

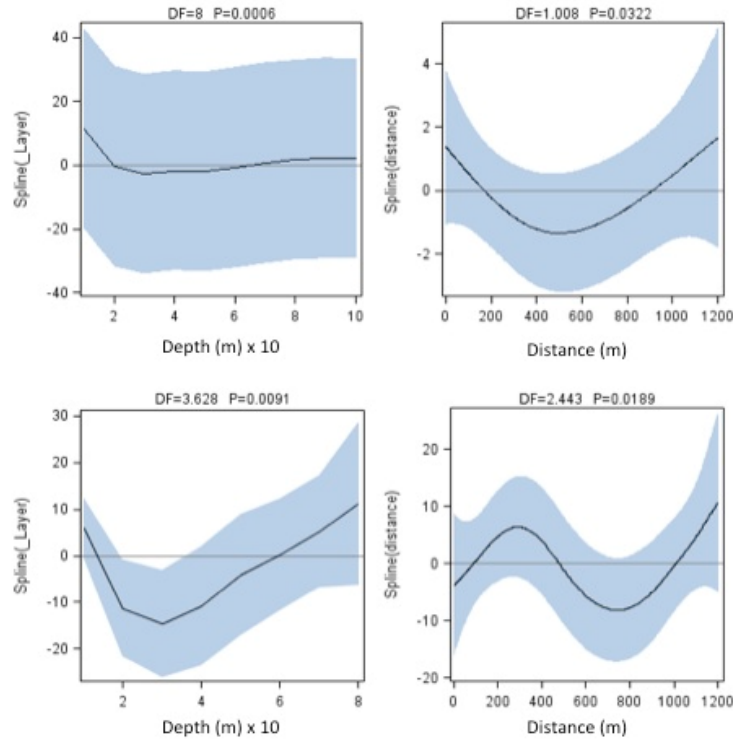


Figure 1.9: Results of the general additive (GAM) model for the large pelagic predator (LPP) class with depth (left column) and distance (right column) from two habitats in the northern Gulf of Mexico. Top panels are standing platforms and bottom panels are toppled platforms. Black line shows the splined relationship with depth or distance and shaded area represents 95% confidence interval.

Table 1.3: Results of the GLM model of the large pelagic predator (LPP) class with habitat and season, with distance as a covariate.

Source	df	F-value	p-value
Habitat	1	1.52	0.22
Season	2	10.38	< 0.0001
Distance	2	0.01	0.91
Habitat x Season	1	5.26	<0.0053
Habitat x Distance	1	0.76	0.38
Habitat x Distance x Season	2	0.30	0.74

not significant at the toppled platforms ($p > 0.05$, GAM). At standing platforms, MVBS of fish was higher in the upper water column at standing platforms, peaking at between 20 and 30 m depth (Figure 1.10). Significant responses with distance were also observed at each habitat ($p < 0.0001$, GAM). The response was similar between habitats, with fish biomass exhibiting an exponential decay with distance, with higher levels of biomass observed within approximately 100 m of the structures (Figure 1.10). Variability was in the model at the standing platforms was higher than at the toppled platforms. The GLM model indicates there are significant differences in MVBS of fish between among seasons ($p < 0.0001$, GLM), but not between habitats ($p > 0.05$) (Table 1.4). Tukey post-hoc testing indicates that fish biomass is higher in the spring and summer than in the winter, and highest at the standing platforms in summer ($p < 0.0001$, GLM).

The zooplankton class also exhibited a significant response with depth and distance based on the GAM model ($p < 0.0001$, GAM). Response with depth differed between habitats, with a peak in zooplankton MVBS at 20 m depth at standing platforms, and highest MVBS at the surface at toppled platforms (Figure 1.11). At both habitats zooplankton MVBS was lowest between 40 and 50 m depth and increased again towards the bottom. The response with distance was similar to that of the fish class, with higher biomass near the structures and exhibiting exponential decline with distance, and reaching background levels at approximately 50 m from the structures (Figure 1.11). The results of the GLM model indicate significant differences in the habitat x season interaction, but not the main effects, and the

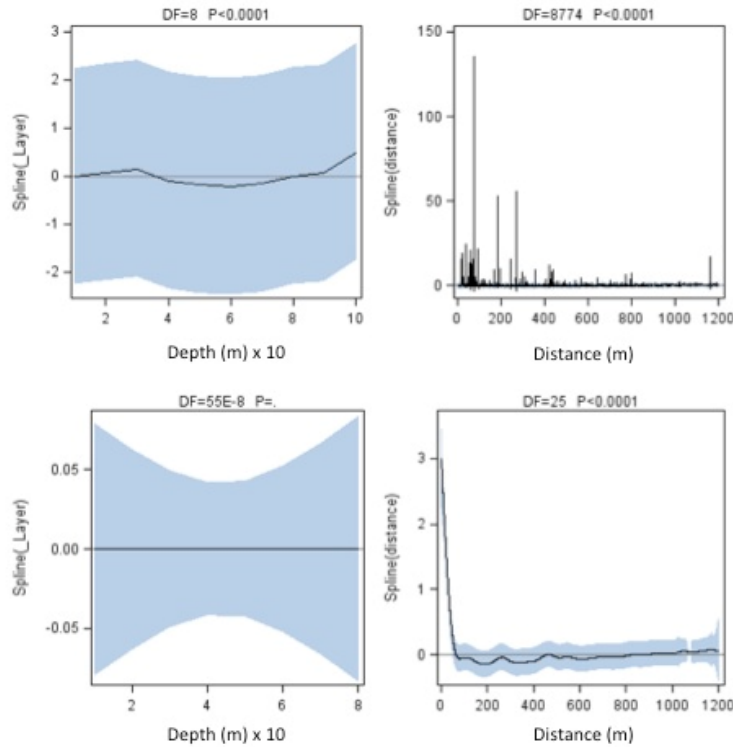


Figure 1.10: Results of the general additive (GAM) model for the fish class with depth (left column) and distance (right column) from two habitats in the northern Gulf of Mexico. Top panels are standing platforms and bottom panels are toppled platforms. Black line shows the splined relationship with depth or distance and shaded area represents 95% confidence interval.

Table 1.4: Results of the GLM model of the fish class with habitat and season, with distance as a covariate.

Source	df	F-value	p-value
Habitat	1	0.04	0.84
Season	2	34.43	< 0.0001
Distance	2	61.78	< 0.0001
Habitat x Season	1	13.56	< 0.0001
Habitat x Distance	1	0.73	0.39
Habitat x Distance x Season	2	5.69	0.0034

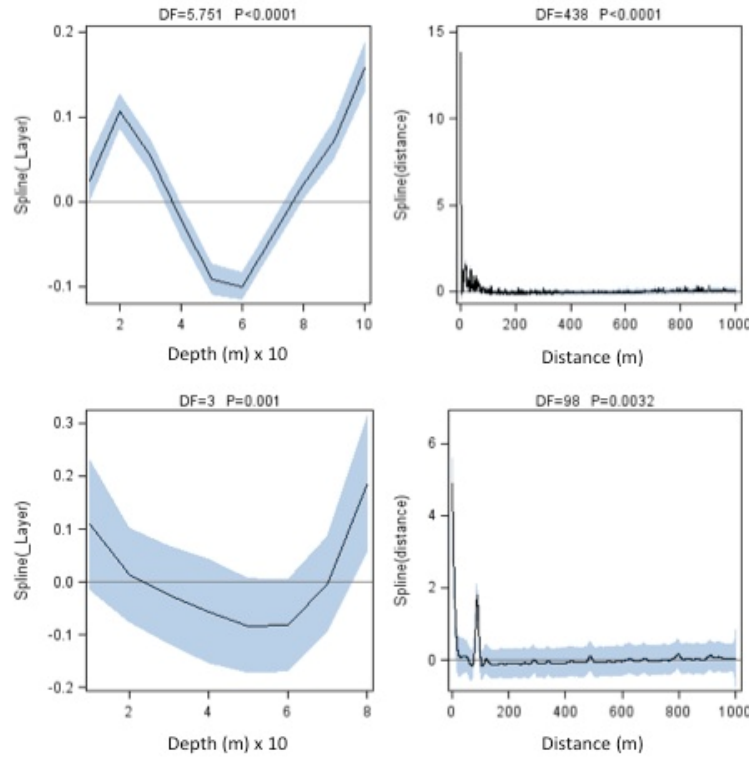


Figure 1.11: Results of the general additive (GAM) model for the zooplankton class with depth (left column) and distance (right column) from two habitats in the northern Gulf of Mexico. Top panels are standing platforms and bottom panels are toppled platforms. Black line shows the splined relationship with depth or distance average and shaded area represents 95% confidence interval.

Table 1.5: Results of the GLM model of the zooplankton class with habitat and season, with distance as a covariate.

Source	df	F-value	p-value
Habitat	1	0.23	0.63
Season	2	2.08	0.12
Distance	2	22.34	< 0.0001
Habitat x Season	1	8.03	0.0003
Habitat x Distance	1	0.04	0.84
Habitat x Distance x Season	2	3.96	0.019

habitat x season x distance interaction (Table 1.5), though MVBS of zooplankton were similar across habitats and seasons.

The SP class was modeled only using a GLM, with no covariate, since distance was removed from the classification. Results of the GLM model indicate significant differences between habitats ($p < 0.0001$, GLM), and seasons ($p = 0.0003$, GLM) (Table 1.6). MVBS of the SP class was nearly four times as high at standing platforms, and three times as high in summer. Pairwise comparisons of the habitat x season interaction indicate the highest MVBS was observed in the summer at standing platforms, though the interaction term was insignificant ($p > 0.05$, GLM, Table 1.6).

Table 1.6: Results of the GLM model of the schooling planktivore (SP) class with habitat and season, with distance as a covariate.

Source	df	F-value	p-value
Habitat	1	15.61	$P < 0.0001$
Season	2	7.91	0.0004
Habitat x Season	2	1.64	0.19

Discussion

Hydroacoustic surveys have been used successfully to examine spatial distributions around large artificial reefs in the GOM (Stanley and Wilson 1996, 1997, 1998, 2000; Boswell et al 2010). However, the key limitation to acoustic surveys is the lack of information on species composition (Simmonds and

MacLennan, 2005), which is an important component of determining how structures such as standing and toppled oil platforms function to the ecology of reef-associated species. This study is one of the first to attempt classification of scatterers based on multifrequency acoustic response. Multifrequency techniques are used regularly for assessment of marine communities in high latitude regions such as the north Atlantic (Korneilussen and Ona 2002; Korneilussen et al. 2009) and the northern Pacific around Alaska (De Robertis et al. 2010), however these regions have much lower species diversity, and there are known target strength values and frequency responses for the majority of the targets observed. The challenge of implementing such a technique in the GOM is the high species diversity associated with the subtropical region, the lack of target strength information, and the close proximity within which many species can associate, particularly on reef habitats, unlike high latitude regions where large single-species schools can stretch for several kilometers. Through visual observation of the site with an ROV, it was not uncommon to see five or more species in the frame at any given point in time (K. Simonsen, personal observation). While some caution should be used in interpreting the results of the classification, as effective groundtruthing of targets was not possible during these surveys, the techniques used here do hold promise for the future of multi-frequency acoustic studies in the GOM. The approach used in this study made it possible to at least identify broad classes of targets, which provide valuable insight into how standing and toppled platforms function as reef habitat.

It is also important to note that analyses were limited to include S_v , the proxy for acoustic biomass, though many studies include estimates of TS, the acoustic proxy for fish length (MacLennan et al. 2002). However, TS values are highly dependent on the species present, orientation, and time of day, among other factors (Simmonds and MacLennan 2005). While general relationships have been developed for TS in a mixed species assemblage (McCartney and Stubbs 1971) and have been used in the Gulf of Mexico (Stanley and Wilson 1997, 1998, 2000, 2003; Boswell et al. 2010), it was not appropriate here because I am not making the assumption that species composition is the same between habitats. Therefore, examining acoustic biomass (S_v) to determine spatial associations with reef structure is more appropriate.

The area of influence found around these structures is larger than that of other studies in the GOM (Stanley and Wilson 1996, 1997, 1998, 2000, 2003; Boswell et al. 2010), but is similar to that of artificial reefs reported in other areas (Gerlotto et al. 1989; Fabi and Sala 2002; Lokkeborg et al. 2002; Soldal et al. 2002; dos Santos et al. 2010). The difference in the area of influence observed here compared to previous studies may be due to the different techniques used, or the location of the structures. Stanley and Wilson (1996, 1997, 1998, 2000, 2003) used stationary hydroacoustics looking outward to determine the area of influence. The difference observed may be due to the detection range of the equipment. Boswell et al. (2010) used similar techniques, however the reef examined in that study was in shallower water (~15 m), and close to shore. The differences in the area of influence reported in these studies may be due to the environment in which the

reefs are located. Overall, MVBS at the sites examined in the current study is similar to that observed by Stanley and Wilson (1996, 1997, 1998, 2000, 2003), and Boswell et al. (2010).

The results of this study indicated higher overall MVBS at standing platforms than at toppled platforms, which is similar to results reported by Wilson et al. (2003). However, differences in distribution between structures were observed only in the upper and middle water column, whereas there was little difference in MVBS in the lower water column, which was also similar to the observations reported by Wilson et al. (2003). While overall MVBS decreased exponentially with distance from the structures, the LPP and SP classes responded much differently with depth, distance, habitat, and season. Both the LPP and SP classes had higher observed MVBS at the standing platforms. Brown et al. (2010) reported high site fidelity of tagged blue runner, a schooling planktivore, at a complex of standing platforms in the northern GOM. The authors hypothesize that the platform structures may benefit the blue runner schools in three ways: potentially providing a mating site, providing elevated food sources, and providing protection from predators. Blue runner are reported to be reproductively active in the summer (McKenney et al. 1958; Goodwin and Finucane 1985; Brown et al. 2010), and the highest biomass of the SP class was observed in the summer months at the standing platforms. The platforms may be aggregating sources of prey, causing higher abundance of the SP class, such as blue runner, as hypothesized by Brown et al. (2010). Higher MVBS of zooplankton was observed near the platform structures, though this may be due to other factors, such as entrained bubbles or currents

around the structures acting to aggregate zooplankton. Furthermore, the lights emitted by the active standing platforms may act to aggregate prey items near the structures (Keenan et al. 2007). Finally, the higher biomass observed at the standing platforms as compared to toppled platforms also supports the notion that platforms are being used for refuge, as the source of refuge is missing from the upper water column at the toppled platforms, which is the preferred habitat for the SP class.

Disproportional abundance of the LPP class was observed, with greater abundance near (< 100 m) the standing platforms and in less than 30 m depth. Hastings et al. (1976) reported high abundance of large pelagic predators such as barracuda, king mackerel, and sharks around platforms in the northern GOM, and the same species were observed in high numbers around the standing platforms examined here as well (K. Simonsen, personal observation). The high abundance of predators around standing platforms may be one reason there is a higher level of background MVBS at distances from the toppled platforms. Biesinger et al. (2011) reported that in the presence of predators, fish will remain close to the home structure, limiting the horizontal extent of migrations for foraging or other reasons. It is likely that the LPP observed at the standing platforms are exerting a top-down control on the system, limiting the horizontal movements of reef-associated fishes.

While spatial distribution of fishes around oil and gas platforms in the GOM has been described previously, (Stanley and Wilson 1996, 1997, 1998, 2000, 2003; Boswell et al. 2010), this is one of the first studies to classify acoustic scatterers in the GOM and examine the spatial distribution of these specific classes. This

information is particularly relevant as more platforms are decommissioned and converted into artificial reefs. One of the proposed benefits of decommissioned platforms as artificial reefs is to maintain fish habitat (Dauterive 2000; Kaiser 2006), however the results of this study show that these structures will differentially affect different species, or classes of reef-associate fishes. The similarities observed in the lower water column between habitats and over seasons indicate that demersal species are likely to be found at both habitats. However, species that tend to occupy the upper water column, such as those in the LPP and SP classes, will likely be found in higher abundance at the standing platforms.

Future studies should find ways to better incorporate the distribution of fish biomass in near field and within the structure of both standing and toppled platforms, such as more extensive ROV or stationary video surveys. Furthermore, this information will help to better groundtruth the acoustic classification developed here. While the classification system was effective, it is limited by the lack of groundtruthed data available. Groundtruthing relied primarily on visual observation of schools and individuals visible at the surface. More extensive video would also help to develop target strength signatures for some commonly observed fishes. This information will be vital to conducting acoustic surveys for quantitative fisheries analyses in the GOM.

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CHAPTER 2: CONTRASTING DIEL MOVEMENT PATTERNS OF REEF-ASSOCIATED FISHES AROUND STANDING AND TOPPLED OIL AND GAS PLATFORMS IN THE NORTHERN GULF OF MEXICO

Introduction

Diel movement and diel vertical migration (DVM) of fishes and zooplankton has been well documented, though there is some debate as to the factors that drive the behavior (Bohl 1980; Lampert 1989; Bollens and Frost 1989; Neilson and Perry 1990; Appenzeller and Leggett 1995). Most studies point to factors such as prey availability, predator avoidance, and bioenergetics as the principal drivers for this behavior, though it is likely that many factors contribute (Lampert 1989; Bollens and Frost 1989; Neilson and Perry 1990; Appenzeller and Leggett 1995; Schabetsberger et al. 2000). Studies have also shown that DVM can be influenced by a number of environmental factors, such as light and temperature, which can affect the extent to which fishes and zooplankton move through the water column (Neilson and Perry 1990; Appenzeller and Leggett 1995; Schabetsberger et al. 2000), and have been experimentally manipulated in the laboratory (Sogard and Olla 1996).

Of particular importance to the diel behavior of fishes is the temporal association with the habitat they utilize, particularly for reef-associated fishes (Jacobsen and Berg 1998; Meyer et al. 2000; Meyer and Holland 2005; Luo et al. 2009; Farmer and Ault 2011). Some species of coral reef fishes are known to hide in reef habitats during the day and make long foraging migrations at night (Meyer et al. 2000; Meyer and Holland 2005). Similarly, grey snapper (*Lutjanus griseus*) were found to spend the day in mangrove habitats, leaving at night to forage in seagrass

beds (Luo et al. 2009). Peabody (2004) found that red snapper (*Lutjanus campechanus*) associating with oil and gas platforms remained near the structures during the day and moved off at night, presumably to make foraging migrations. Conversely, McDonough (2009) found that red snapper remain close to large artificial reefs (oil and gas platforms) at night, leaving during the day, presumably to forage.

Understanding the movement patterns of reef-associated fishes around artificial reefs is important to our understanding of how these structures function in the ecology of these species. This is especially true in the northern Gulf of Mexico (GOM), which is home to approximately 3000 oil and gas platforms, creating the largest *de facto* artificial reef deployment area in the world. In addition to these standing oil and gas platforms, approximately 300 structures have been toppled and converted into artificial reefs in one of nine planning areas along the Louisiana continental shelf (Wilson and Van Sickle 1987). It is important to understand how these structures affect the behavior and community dynamics of reef-associated fishes. One of the prevailing theories is that reef-associated fish species move off the structures at night to forage (McCawley and Cowan 2007; Wells et al. 2008; Shipley and Cowan 2010; Biesinger et al. 2011; Campbell et al. 2011; but see McDonough 2009). Diel differences in abundance of reef-associated fishes have been observed around artificial reefs in the North Sea (Soldal et al. 2002), the Mediterranean Sea (Fabi and Sala 2002), and in the Gulf of Mexico (Stanley and Wilson 2003; McDonough 2009; Shipley and Cowan 2010). In general, observations of diel variability in fishes have reported peaks in biomass from around midnight to

between 2 and 6 am (Schabetsberger et al. 2000; Benoit-Bird et al. 2001; Soldal et al. 2002; Fabi and Sala 2002; Stanley and Wilson 2003). This may be a behavior adapted to avoid visual predators, especially around artificial reefs, which are known to aggregate predators (Hastings et al. 1976; Bohnsack 1989; Bohnsack et al. 1997; Grossman et al. 1997; Lindberg 1997; Bortone 1998; Stanley and Wilson 1996, 1997, 1998, 2000, 2003).

Previous studies of diel movement of fishes associated with oil and gas platforms in the GOM have resulted in conflicting results as to the diel movements of reef-associated fishes. These studies have relied on stationary hydroacoustics (Stanley and Wilson 2003; Wilson et al. 2003) and acoustic telemetry (Peabody 2004; McDonough 2009). Stanley and Wilson found significantly higher fish density at midnight at three different platforms in the GOM, though Wilson et al. (2003) found higher biomass at dusk at a different platform. In a study of acoustically tagged red snapper, Peabody (2004) observed diel movement away from platforms at night, which the author attributed to foraging excursions. In a similar study, McDonough (2009) observed a different pattern of diel periodicity in red snapper movement, with movement over greater distances during the day but a greater number of detections near the platforms at night. This difference was also interpreted as diel feeding behavior, but here it was determined that red snapper remaining close to the structures during the night, and ventured out to feed during the day. While these studies provide useful insight, they are limited spatially by the extent of possible detection. Wilson et al. (2003) utilized a mobile hydroacoustic approach to examine toppled platforms in the GOM, though their results were

somewhat conflicting. Two toppled platforms were examined, one of which had higher fish biomass at midnight, and one that had low fish biomass at midnight, with high biomass at dawn.

The goal of this study was to examine the diel movement of reef-associated fishes around standing and toppled oil and gas platforms using a mobile hydroacoustics approach. Hydroacoustics is a useful tool to assess distribution of organisms associated with spatially heterogeneous habitats, as it provides a noninvasive technique to acquire data over a large area with higher spatial resolution than traditional sampling gears (Stanley and Wilson 1997, 1998, 2001; Benoit-Bird et al. 2001; Simmonds and MacLennan 2005; Boswell et al. 2010). Furthermore, data can be collected over extended periods of time to examine distributions on a finer temporal scale than traditional sampling gear (Simmonds and MacLennan 2005).

The prevailing theory is that reef-associated fishes stay close to the platforms during the day and make foraging migrations at night (Peabody 2004; Shipley and Cowan 2010; Campbell et al. 2011; but see McDonough 2009), thus the goal of this study was to attempt to quantify this movement with a hydroacoustic approach as there is a paucity of information at these scales in the literature.

Methods and Materials

Two standing oil and gas platforms (hereafter standing) and one decommissioned and toppled oil and gas platforms (hereafter toppled) were examined in this study. Toppled platforms have the surface deck structures and

infrastructures removed, are cut approximately 30 m below the surface, and the remaining structure is placed on the seafloor adjacent to the platform base (Kaiser 2006). Study sites were located in the Eugene Island (EI) block of the Louisiana coast in the northern Gulf of Mexico (GOM) (Figure 2.1). The toppled platform was EI 322 and was sampled in two consecutive years, 2009 and 2010. Standing platforms included EI 325 and EI 314. EI 325 was sampled in 2009 and EI 314 was sampled in 2010, and was included opportunistically in conjunction with two other sampling efforts (Boswell et al. unpublished data; Harwell unpublished data). Sampling was conducted in June of both 2009 and 2010 to maintain temporal consistency and avoid seasonal bias. All sites are located in approximately 70 m water depth.

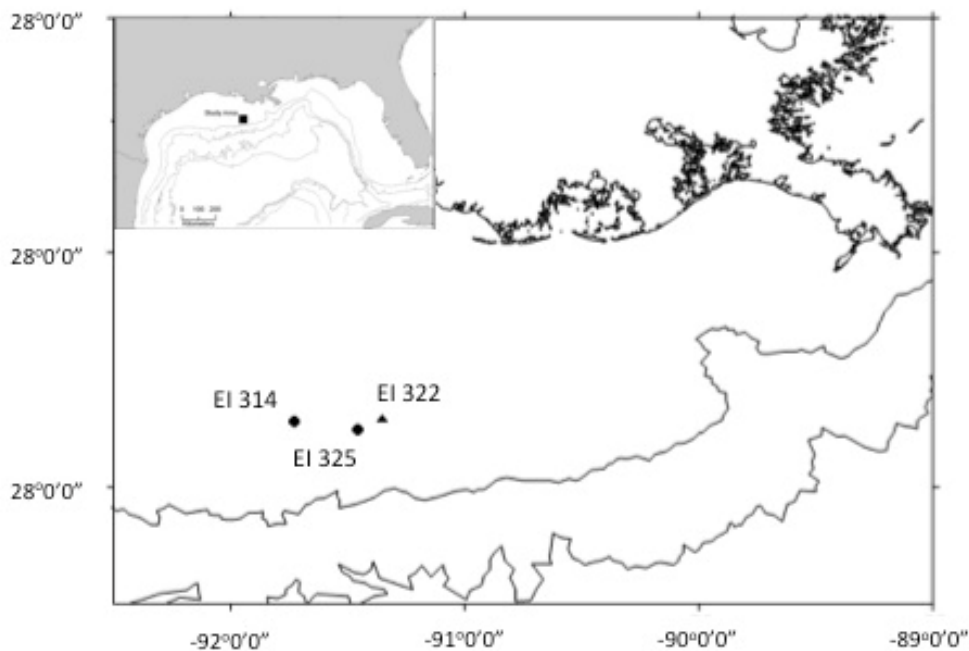


Figure 2.1: Sampling locations for acoustic data collection in the Eugene Island (EI) block of the northern Gulf of Mexico. Sites include two standing (circles) and two toppled (triangles) oil and gas platforms.

Environmental data were collected once per day from surface to bottom at each site during sampling with a Sea-Bird SBE 25 CTD profiler. Eight CTD casts were conducted in a transect running north to south at each site at distances of 1.5, 1.0, 0.5, and 0.25 km both north and south of the platform structure. Water quality parameters collected include conductivity, temperature, pressure, depth, salinity, dissolved oxygen and optical backscatter. Values of temperature, salinity, and dissolved oxygen were examined at each habitat and each year for comparison with fish distribution

Acoustic backscatter data were collected using a BioSonics acoustic echosounder equipped with three downward-looking split-beam transducers (70, 120, and 200 kHz), calibrated by the standard sphere method (Foote et al. 1987). Data were collected at a threshold of -100dB, with a pulse duration of 0.4ms. The vessel was equipped with a bulbous bow and kort nozzle propellers, which were designed to provide a smoother ride and reduce the level of acoustic background noise produced by the ship. Surveys were conducted at an average speed of 2 m s⁻¹ and each transect was approximately 3 km in length, with the reef structure at the midpoint. Transects were run at each site for approximately 48 continuous hours, conducted in a circular pattern, with each transect offset 18° from the previous line (Figure 2.2). Transducers were mounted on a pivoting boom that was lowered when on site, extending approximately 2 m depth below the surface to avoid bubbles entrained in the ships wake.

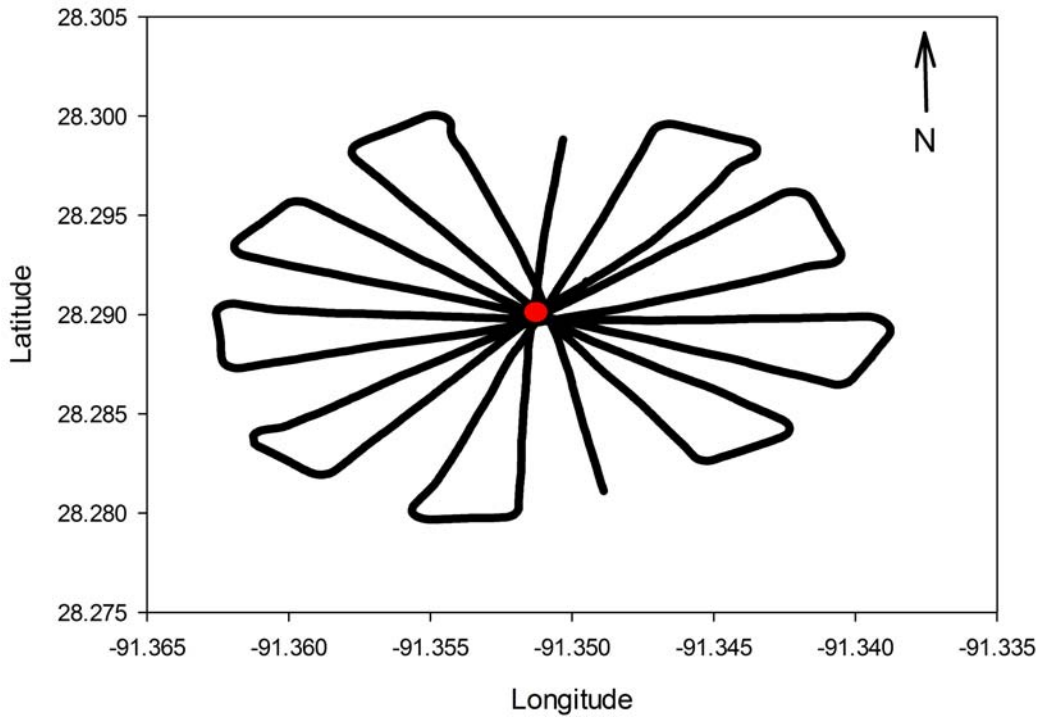


Figure 2.2: Approximation of cruise track used during acoustic sampling. Red circle represents geographic center point of reef structure.

Acoustic backscatter data were post-processed using Echoview v. 5.3 (Myriax Pty. Ltd., Hobart, Tasmania, Australia) to obtain values of mean volume backscatter (S_v) and nautical area scattering coefficient (NASC). Analysis thresholds were set in Echoview for S_v , and calibration settings were applied to compensate for the effects temperature and salinity on speed of sound. All echograms were visually inspected to exclude regions of bad data (i.e., signal loss, noise). Data within 2 m of the transducer face was excluded to account for surface noise, transducer ringdown and near field effects. A bottom detection algorithm with a 0.5m backstep (Ona and Mitson 1996) was applied to exclude the seafloor and reef structures from the

analysis and then manually edited as needed. Mean volume backscattering strength (MVBS; S_v , dB) data, integrated at 10 m depth by 10 m distance bin, were exported from Echoview and used for analysis of spatial and temporal distribution of the fish community around platform habitats. MVBS represents the total integrated energy of targets in the water column and the intensity of backscattered energy is understood to be proportional to the biomass of nekton in the water column (Simmonds and MacLennan 2005).

Acoustic targets were classified into representative groups (i.e, fish, zooplankton) within the echograms in Echoview through the process of dB differencing, using the 120 kHz and 70 kHz transducers. Swim-bladdered fish are known to have decreasing values of S_v with increasing frequency (Korneilussen and Ona 2002; Korneilussen et al. 2009; de Robertis et al. 2010), while fish lacking swim bladders are relatively frequency independent at lower frequencies, with a sharp increase at 200 kHz (Korneilussen and Ona 2002; Korneilussen et al. 2009). For this reason, the 70 kHz and 120 kHz frequencies are most appropriate for differentiating between fish and zooplankton scatterers following Madureira et al (1993), Korneilussen and Ona (2002), Mosteiro et al. (2004), Korneilussen et al. (2009) and De Robertis et al. (2010). First, 120 kHz and 70 kHz echograms were matched in time to assure that samples were temporally coincident. Following this, background noise and intermittent noise spikes were suppressed within in Echoview following methods described in De Robertis and Higginbotham (2007). Frequency response differencing was achieved by subtracting each sample at 70 kHz from the corresponding sample at 120 kHz (Figure 3). The resulting data were classified into

two groups based on the relative frequency response where sample $S_{v\ 120-70}$ ranging from -15 to 1, was labeled as swimbladdered fish (Madureira et al. 1993; Korneilussen and Ona 2002; Mosteiro et al. 2004; Korneilussen et al. 200; De Robertis et al. 2010) and sample $S_{v\ 120-70}$ ranging from 3 to 25, was classified as zooplankton (Madureira et al. 1993; Korneilussen and Ona 2002; Korneilussen et al. 200; De Robertis et al. 2010)(Figure 3).

Data Analysis

Environmental data were post-processed using SeaBird SBE Data Processing Software v 7.22.4 (Sea-Bird Electronics, Seattle, WA, USA). Mean values of temperature, salinity, and dissolved oxygen were compared with depth between habitats and years with a multiple analysis of covariance (MANCOVA), using depth as a covariate (SAS v. 9.2, Cary, North Carolina, USA).

Mean volume backscattering strength (MVBS) was linearized and compared between habitats, as a factor of depth, and with hour of the day using a mixed model (SAS v. 9.2, Cary, North Carolina, USA), with MVBS used as dependent variable in the model. A second model was run at five discrete distance intervals to examine diel movement of fishes at various distances from the platform structures. The geographic midpoint of each reef structure was determined, and horizontal distance was calculated for each data point from that geographic mean and binned over 10 m intervals to 200 m, with subsequent intervals at 200, 500, 750, 1000, 1250, and 1500 + m. Distance intervals used for this analysis included < 20 m, 50 – 60 m, 100 m, and 500 m, and were selected based on results Chapter 1. The 10 and 20 m

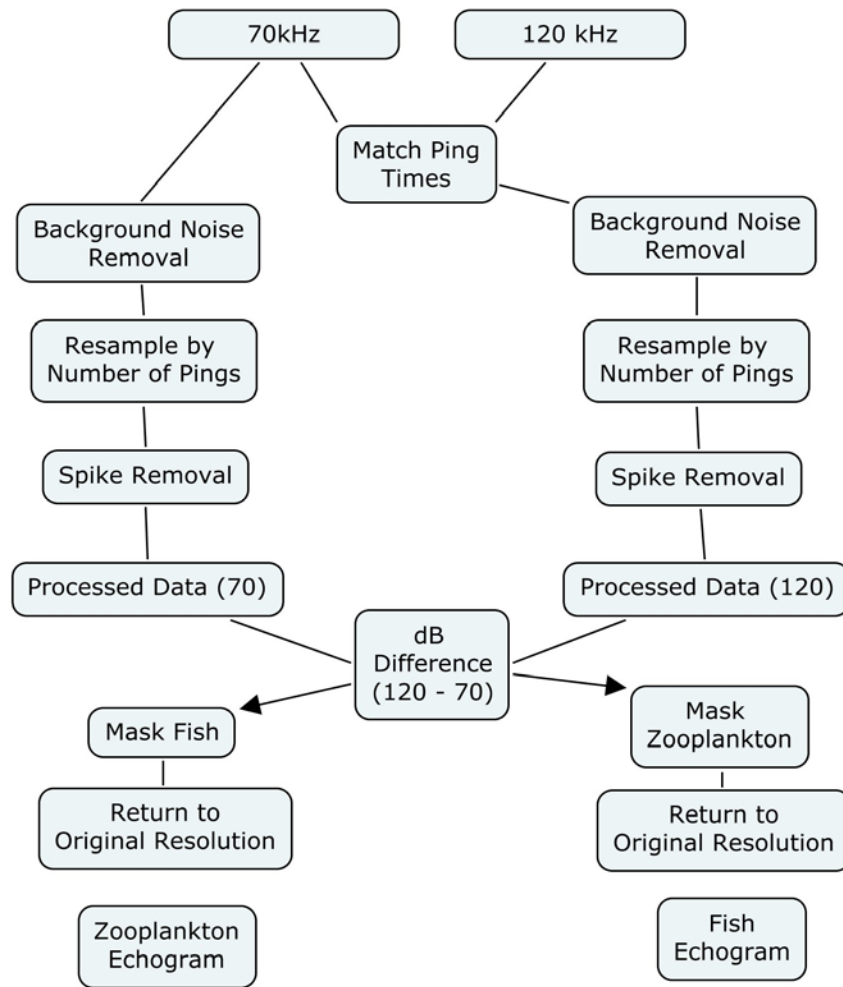


Figure 2.3: Schematic of the Echoview Data Flow used in processing of acoustic data.

distance bins were combined due to low sample size at close distances, especially at the standing platforms where it was not always safely possible to get within 10 m of the structure. The 50 and 60 m distance bins were combined to ensure all depth bins were included in the analysis. Depth bins were further combined from 0 – 30 m, 30 – 60 m, and 60+ m for statistical analysis to examine differences in the upper, middle and lower water column based on differences reported in Stanley and Wilson (1998).

Diel periodicity was examined using both a LOESS regression and a Fast Fourier Transformation (FFT) of MVBS data. The LOESS regression is a nonparametric regression technique that determines the “local” regression based on the chosen interval of the independent variable (hour of the day). MVBS data were regressed by hour to determine when peaks in MVBS occurred during the day. Following the LOESS regression, periodicity in MVBS was examined by performing a Fast Fourier Transformation (FFT) on the MVBS to estimate the temporal patterns in signal intensity of the data. FFT converts the data into power, binned over the sampling time period at which data were collected (1 hr), and is then converted to a sampling frequency, based on the number of observations using the formula:

$$f = (i + 1) * df$$

where i is the sample period (hours 0 to 23), and df is the 1 hour time interval (1/24, 2/24, 3/24,..., 24/24). Each value represents the number of cycles that occur in a day (cycles*d⁻¹) with 1 cycle*d⁻¹ representing the diel signal. MVBS was averaged over each hour of the day at each habitat and depth interval (upper, middle and lower water column), then Fourier-transformed and plotted against the f value to examine power over time. Calculations were all completed in MATLAB (v. R2007a).

Following the habitat comparison, data were again divided into distance intervals and the same technique was applied to examine periodicity at discrete distances from each habitat. For this analysis, only the 50-60, 100 and 500 m distance bins were used. Fourier transformations are sensitive inconsistencies in the data, and at the closest distance bin (10 – 20 m) there were a large number of

missing data points over time and depth due to sampling in close proximity to the structure, necessitating the exclusions of this interval from analysis. The distance intervals selected therefore represent a near, intermediate, and far distance from the platform to examine diel periodicity.

Results

CTD data suggests a strong thermocline and halocline were present during the sampling events, based on sharp declines in temperature and increase in salinity (Figure 2.4). Levels of DO initially increased with depth, and then decreased toward the bottom, however the region did not become hypoxic ($< 2 \text{ mg} \cdot \text{L}^{-1}$) during the sampling period. Results of the MANCOVA indicate that temperature, salinity, and DO were all significantly different between years ($p < 0.0001$, MANCOVA), but were not significantly different between habitats ($p > 0.05$). Depth was a significant covariate for all independent variables ($p < 0.0001$, MANCOVA).

Results of the mixed model indicated significant differences in MVBS with habitat, depth, and time of the day ($p < 0.0001$, Mixed model, SAS, Table 2.1). MVBS exhibited a diel pattern, which differed between depth bins, and habitats (Figure 2.5). At standing platforms, MVBS changed two-fold during the course of the day, with higher MVBS in the upper and middle water column at night, and higher MVBS in the lower water column during the day (Figure 2.5). At toppled platforms, the pattern was similar in the middle and lower water column while MVBS remained high in the upper water column. Changes in MVBS occurred between 0500 and 0600 hours, and again between 1800 and 2000 hours, with lowest MVBS observed

during the crepuscular periods across all habitats and depths. The changed observed during the crepuscular period was also observed in the LOESS regression, which indicates declines in MVBS at 0500 and increases between 1800 and 2000 hours (Figure 2.6).

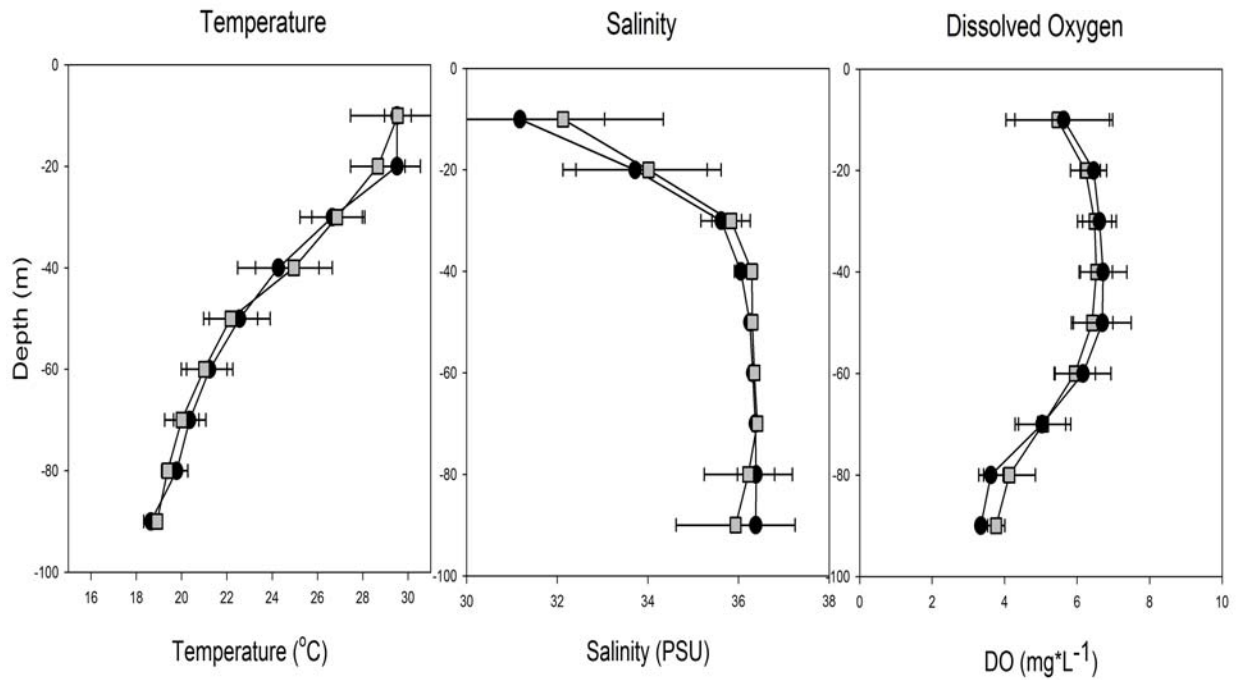


Figure 2.4: Environmental data collected from CTD casts at standing (black circle) and toppled (grey square) oil and gas platforms in the northern Gulf of Mexico. Temperature (in degrees C), salinity (in PSU) and dissolved oxygen (DO, in mg·L⁻¹) are shown plotted against depth.

Table 2.1: ANOVA table type III fixed effects from the mixed model comparing MVBS with habitat, season, depth, and distance. Significance was set at $\alpha = 0.05$ for all tests.

Source	df	F-value	p-value
Habitat	1	278.45	< 0.0001
Depth	2	214.50	< 0.0001
Hour	23	32.76	< 0.0001
Habitat x Depth	2	208.53	< 0.0001
Habitat x Hour	22	32.59	< 0.0001
Depth x Hour	46	32.94	< 0.0001
Habitat x Depth x Hour	44	34.37	< 0.0001

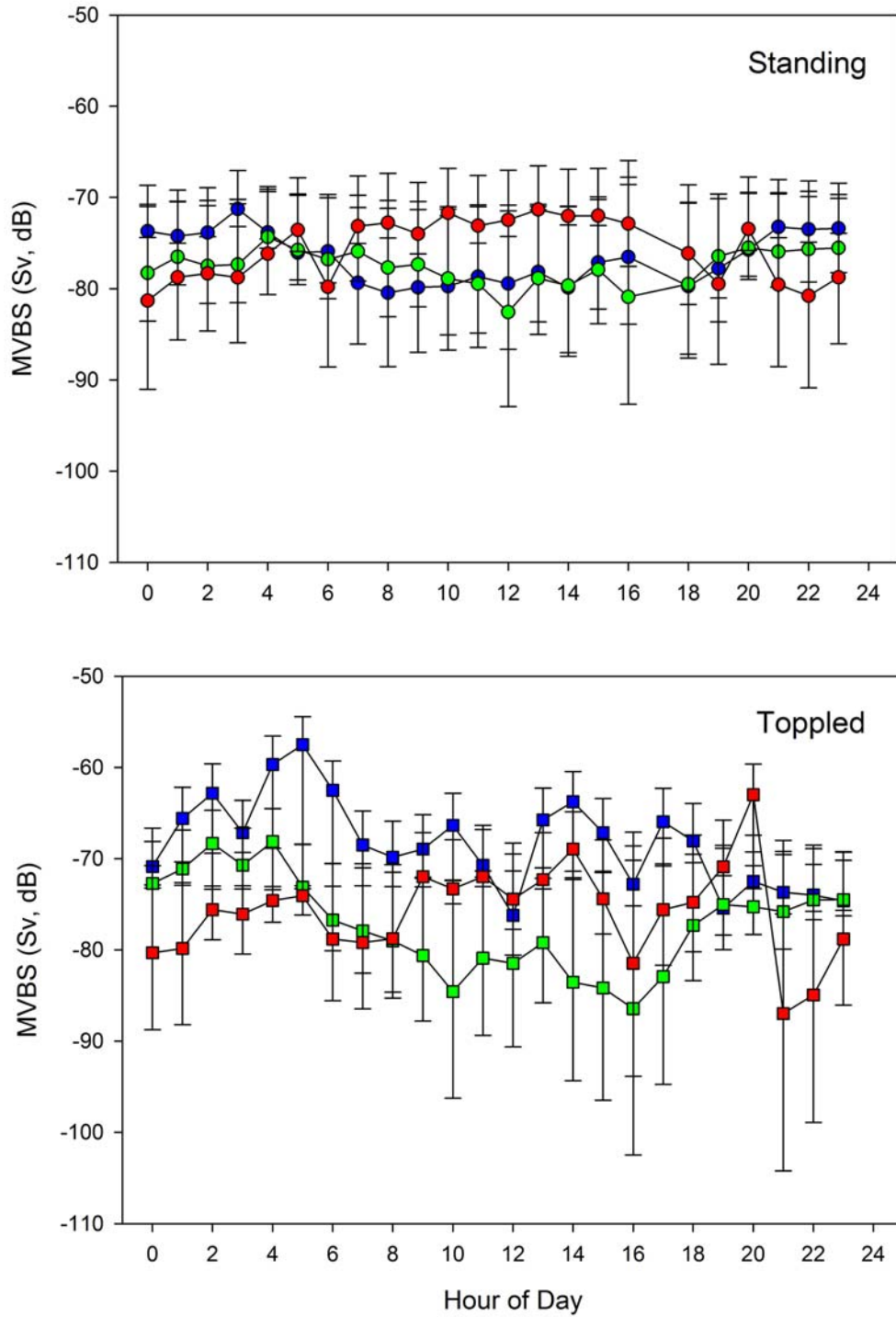


Figure 2.5: MVBS at two habitats in the northern Gulf of Mexico over a 24-hour period. Circles represent standing oil and gas platforms (upper panel) and squares represent toppled oil and gas platforms (lower panel). Blue symbols are upper water column (0 – 30 m), green symbols are middle water column (30 – 60 m), and red symbols are lower water column (> 60 m). Standard error bars are shown.

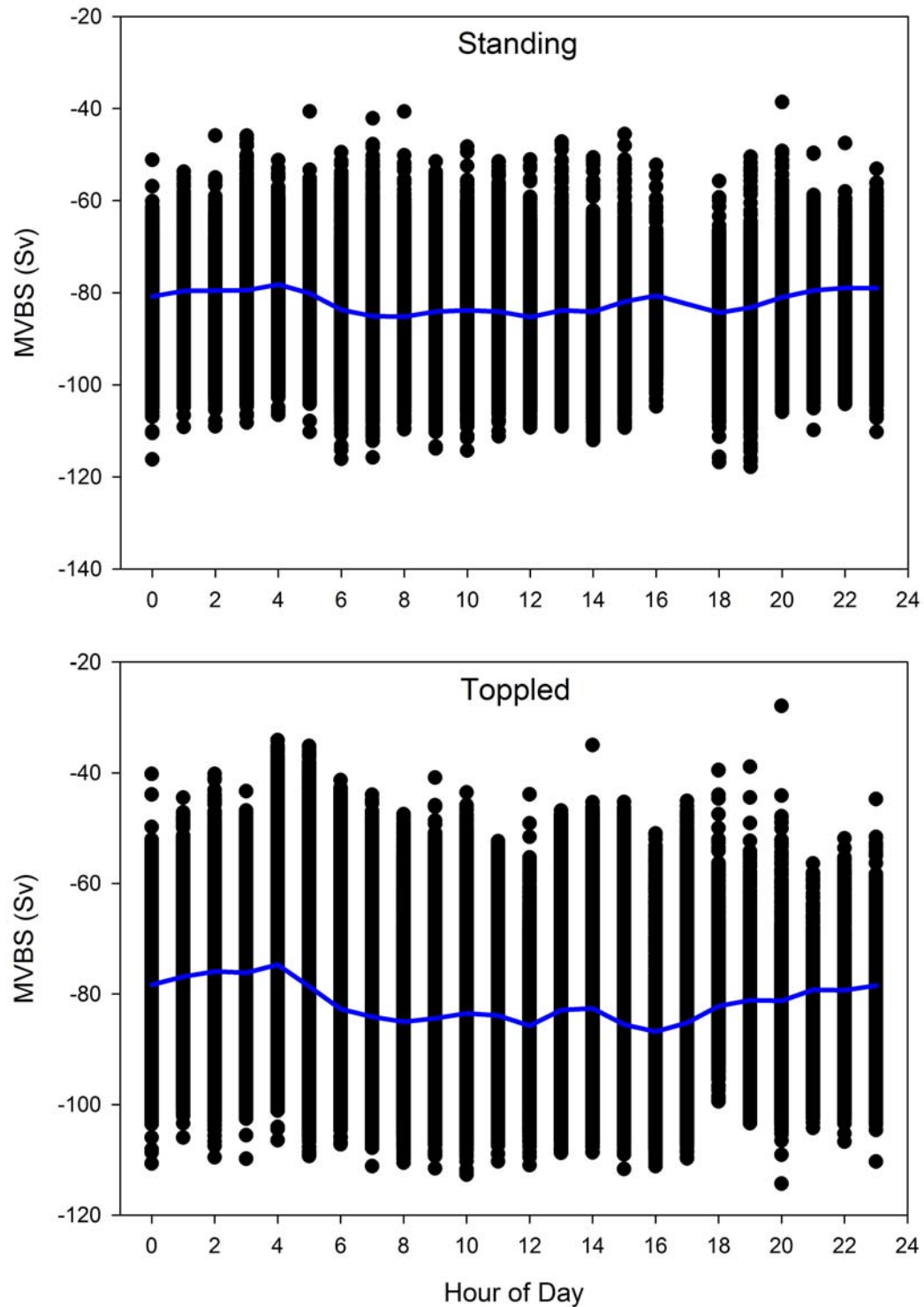


Figure 2.6: Actual mean volume backscatter (MVBS) values (black circles) and LOESS predicted value (blue line) of MVBS for each hour of the day at two habitats in the northern Gulf of Mexico including standing (upper panel) and topped (lower panel) oil and gas platforms.

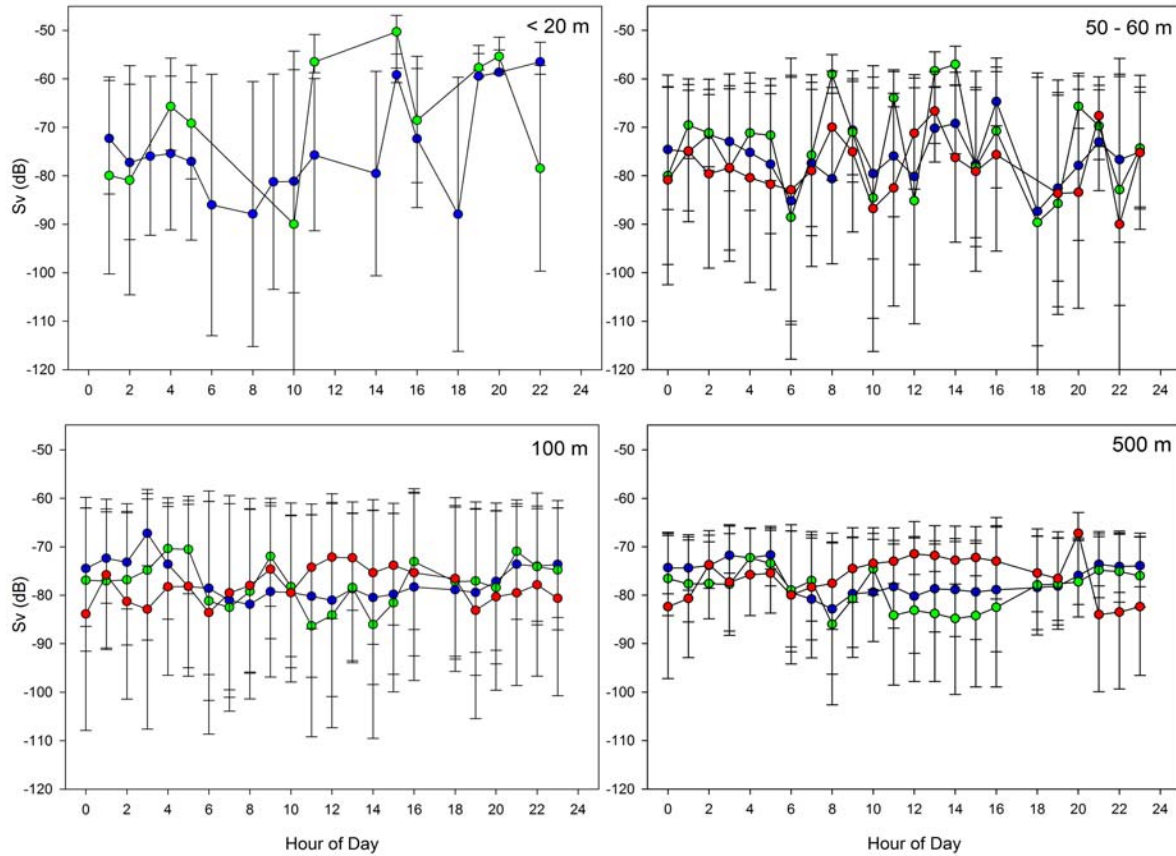


Figure 2.7: MVBS at standing oil and gas platforms in the northern Gulf of Mexico over a 24-hour period at four different distances from the reef structure: < 20 m, 50-60 m, 100 m, and 500 m. Blue symbols are upper water column (0 – 30 m), green symbols are middle water column (30 – 60 m), and red symbols are lower water column (> 60 m). Standard error bars are shown.

The observed diel pattern was variable with distance and results of the mixed model indicated significant differences with distance, habitat, and hour of the day ($p < 0.0001$, Mixed model, SAS). At the standing platform sites at distances less than 20 m, there was little discernable diel pattern in MVBS, though sample size at this distance is low compared to the other distance bins. At the 50 – 60 m distance bin, MVBS is highly variable, and fluctuated throughout the day, though no discernable diel pattern was detected (Figure 2.7). At the 100 m distance bin, the diel pattern was more apparent, with higher MVBS in the upper and middle water

column at night, and higher MVBS in the lower water column during the day (Figure 2.7). At 500 m, there is a strong diel signal in MVBS at all depths, which closely resembled the diel pattern over all distances combined (Figure 2.5).

At the toppled platforms MVBS is consistently high and variable at all distances. At the < 20 m distance interval, MVBS was relatively consistent in the upper water column, and a weak diel pattern was detected in the middle water column, though sample size here is low (Figure 2.8). At the 50 – 60 m distance bin, there was a discernable diel pattern in MVBS, particularly in the middle and lower water column, though sample size was relatively low in the lower water column due to the presence of the toppled reef structure. At 100 m, the diel pattern was detected in the middle and lower water column, and at 500 m distance, a strong diel pattern was detected in the middle and lower water column (Figure 2.8), which again resembles the diel pattern over all distances combined (Figure 2.5).

Fourier transformation indicated a strong diel periodicity at both habitats and at all depth bins, with highest power at the frequency of 1 cycle*day⁻¹ (Figure 2.9). The power of this diel periodicity was stronger at the toppled platforms particularly in the upper and middle water column, indicating a stronger diel signal. The Fourier transform showed a lot of noise past the frequency 1 cycle*day⁻¹, indicating that over the entire study site most of the variability can be explained by the diel cycle.

Diel periodicity was dependent on distance from the structure as indicated by the power analysis by distance, particularly at the standing platforms. At close ranges (50 – 60 m), there is no obvious pattern in the power analysis, and no strong

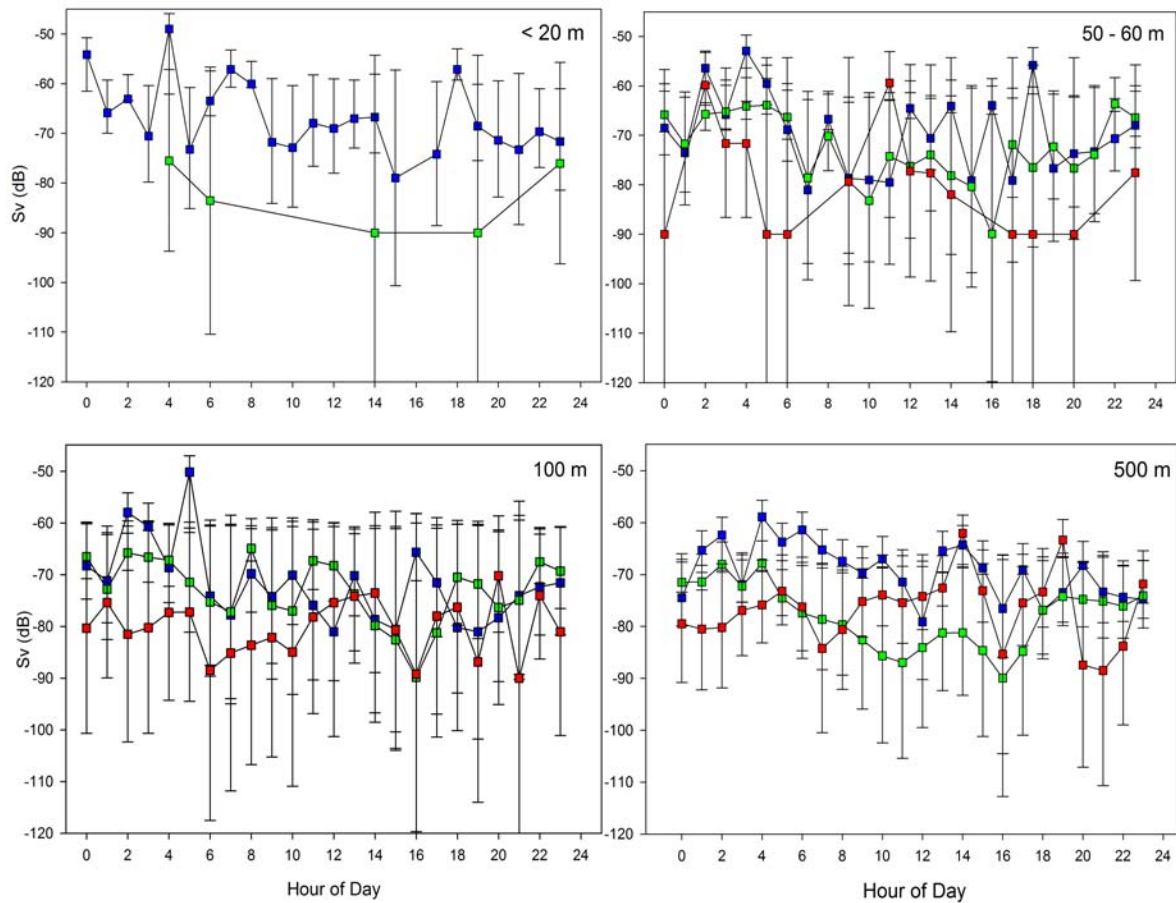


Figure 2.8: MVBS at toppled oil and gas platforms in the northern Gulf of Mexico over a 24-hour period: < 20 m, 50-60 m, 100 m, and 500 m. Blue symbols are upper water column (0 – 30 m), green symbols are middle water column (30 – 60 m), and red symbols are lower water column (> 60 m). Standard error bars are shown.

peak at the frequency of $1 \text{ cycle} \cdot \text{day}^{-1}$, indicating the diel cycle (Figure 2.10). The results are also variable by depth with no discernable pattern emerging. At 100 m distance there is a weak diel signal. The results are also variable with depth, and there is a lot of noise in the signal. By 500 m distance the strong diel signal appears, which is consistent by depth, and the results resemble the analysis of the overall study site. At the toppled platforms, there is a strong diel signal at all distances,

except the lower water column at 50 – 60 m, which this is likely due to low sample size and high variability in the data for that region (Figure 2.10).

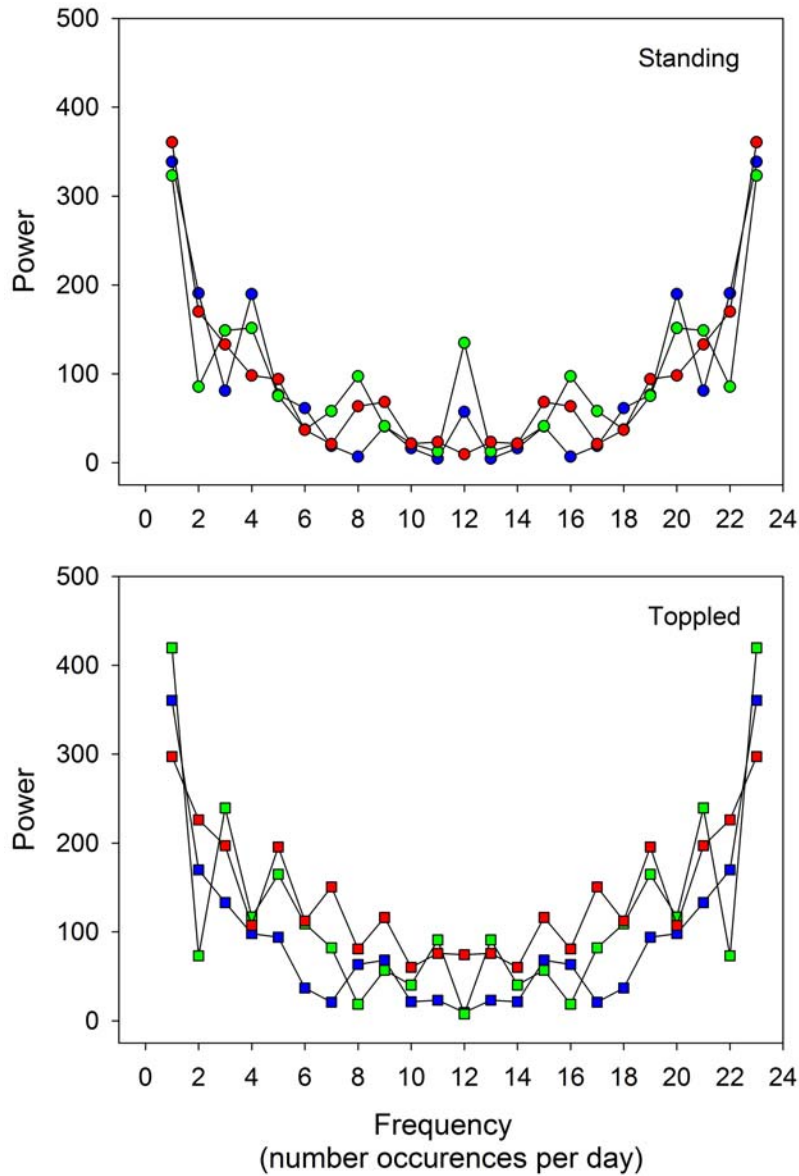


Figure 2.9: Periodogram of Fourier-transformed acoustic signal from two habitats in the northern Gulf of Mexico including standing and toppled oil and gas platforms. Three depth bins are shown separately. Blue represents upper (0 – 30 m), green represents middle (30 – 60 m), and red represents lower (> 60 m) water column.

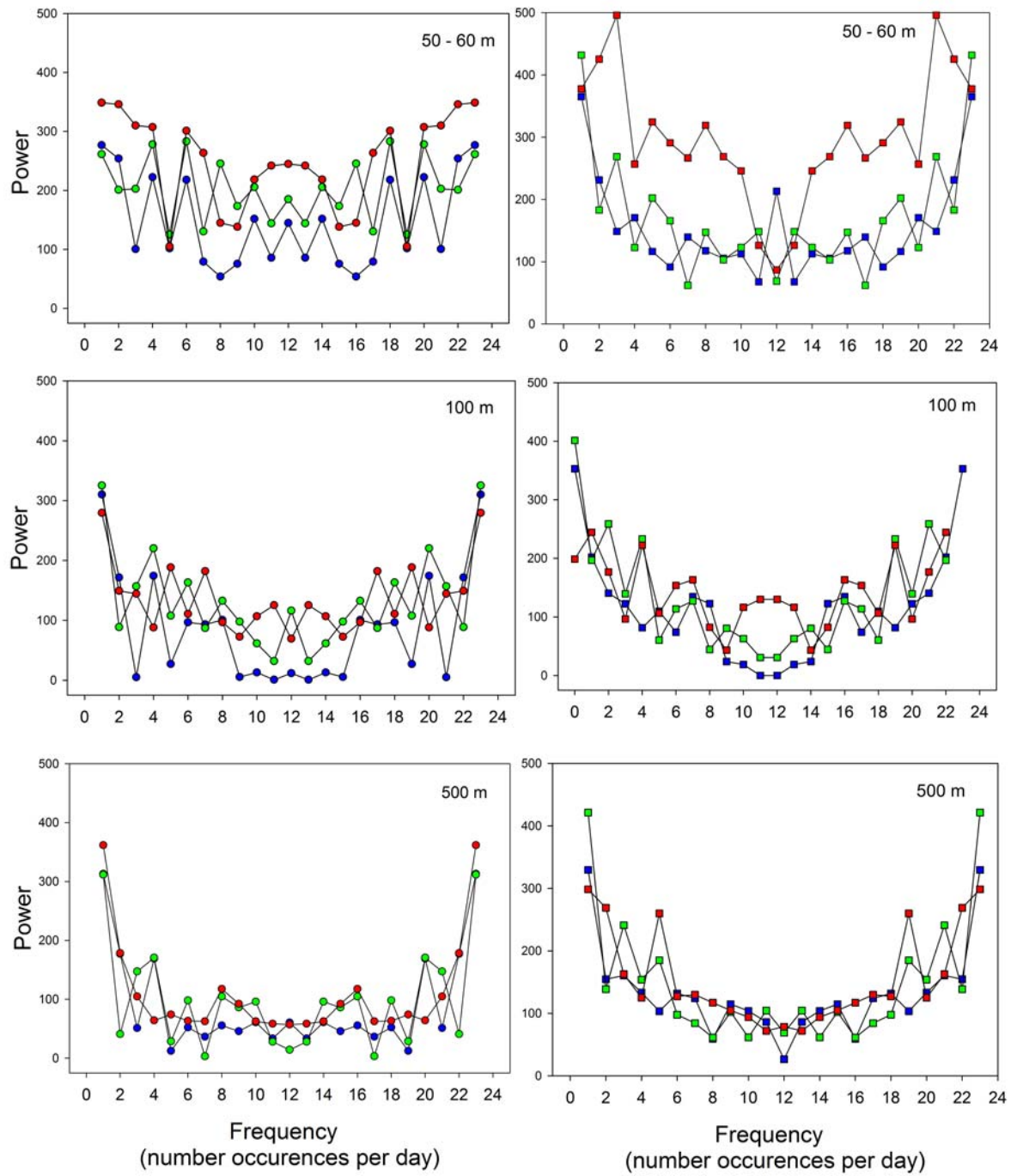


Figure 2.10: Periodogram of Fourier-transformed acoustic signal from three distance bins at two habitats in the northern Gulf of Mexico including standing (left panel) and toppled (right panel) oil and gas platforms. Upper panels represent 50-60 m from the structures; middle represents 100 m from the structures and lower represents 500 m from the structures. Three depth bins are shown separately. Blue represents upper (0 – 30 m), green represents middle (30 – 60 m), and red represents lower (> 60 m) water column.

Discussion

Diel periodicity in fish and zooplankton distribution has been well documented in the literature, however few studies have attempted to describe the diel nature of movement at the community level across scales of several km. Moreover, this study incorporates additional complexity in evaluating variation in habitat association across four dimensions (spatial and temporal) in an oceanic setting. Previous attempts to quantify diel movement have been limited in space and time (McDonough 2009; Stanley and Wilson 2003). McDonough (2009) found strong diel periodicity in the movement of red snapper, however the study was limited only to one species, and was limited by the detection range of the autonomous receiver (approximately 350 m from the platform). Stanley and Wilson (2003) used a stationary hydroacoustic approach to detect diel periodicity in fish biomass around oil and gas platforms, though data was only collected at four discrete times during the day (dawn, noon, dusk, midnight) for 2 hours at a time. Mobile hydroacoustic techniques have been successfully utilized to examine spatial distributions of reef-associated fishes in the GOM (Boswell et al. 2012; also see Chapter 1).

The results of this study indicate that there is a strong diel pattern in distribution of fishes around oil and gas platforms, which is dependent on habitat, depth and distance from the reef structures. MVBS was generally higher at night in the upper and middle water column, and higher during the day in the lower water column. Wilson et al. (2003) found mixed results with time of day around two toppled platforms. One platform had highest fish biomass at midnight, while the

other had low biomass at midnight at high biomass at dawn. The authors also reported highest biomass at a standing platform during crepuscular periods, based on a fixed, outward-looking hydroacoustic array. Conversely, Stanley and Wilson (2003) found significantly higher biomass around standing platforms at midnight, based on a similar fixed, outward-looking hydroacoustic array, corresponding the patterns in the upper water column in this study. Such behavior is often attributed to avoidance of visual predators during daylight hours. Additionally, McDonough (2009) observed that red snapper made large movements during the day, dispersing from the platform structure, and making larger movements at depth. While McDonough (2009) only examined one species, red snapper are found in high abundance at oil and gas platforms, and the pattern observed agrees with the current findings of higher biomass in the lower water column during daylight hours. This behavior may be common to other reef-associated fishes with similar demersal feeding strategies. Interestingly, this behavior is opposite of that reported by Peabody (2004) on red snapper around oil and gas platforms in the GOM, and on closely related species (grey snapper) observed elsewhere (Luo et al. 2009), which suggest that reef-associate species forage away from sheltered habitat at night. Visibility in the lower 30 m of the water column is often reduced due to the resuspension of soft-bottom sediments and the presence of a nepheloid layer, resulting from Mississippi River runoff (McGrail and Carnes, 1983), based on observations of ROV footage at the sites. The reduced visibility may make it easier for reef-associated fishes to avoid predation during the day (Biesinger et al. 2010), while taking advantage of the higher biomass of potential prey near the bottom.

Distance from the structure had a profound effect on the diel periodicity of the associated fish community, particularly at the standing platforms. This was most evident at distances less than 100 m from the structures, where there was a near complete breakdown of diel periodicity. This is most likely attributable to light being emitted from the active platforms examined in this study. Keenan et al. (2007) found that the light field around oil and gas platforms in the GOM can extend out to 100 m (or more depending on size of the structure) from the platform structure, and to over 20m in depth which is within the “area of influence” of the reef structure, or the area of high biomass associated with the platform (Stanley and Wilson 1996, 1997, 1998, 2000, 2003; Wilson et al. 2003; Boswell et al. 2010; also see Chapter 1). Based on these results, and those shown by Keenan et al. (2007), the light field surrounding oil and gas platforms may have a significant impact on the associated fauna. One way this is possible is to increase feeding opportunities for visual predators, making these habitats less suitable for reef-associated fishes. In general, MVBS of fishes was higher at standing platforms than at toppled platforms, based on the results of Chapter 1. This may be due to the attraction of schooling planktivores and large visual predators to the light field. The light field and the presence of large visual predators may be disrupting diel movements in fishes closely associating with the standing platform structures. Biesinger et al. (2010) showed that in areas of high predation pressure, fish will make less frequent and shorter foraging migrations, such as those typically made on a diel cycle, until resources are depleted.

At the toppled platform, the diel periodicity was more consistent, even at the closest distances from the reef structure. There was some evidence of diel periodicity within 20 m of the structure, though due to small sample size and inconsistency with depth, this result is inconclusive. At 50 – 60 m from the reef structure, diel periodicity was evident, unlike the standing platforms. This was particularly true for the middle and lower water column, whereas the upper water column had consistently high levels of MVBS. This higher level of MVBS in the upper water column was likely due to the presence of large schools of bonito (*Euthynnus* sp.) visible at the surface at dusk and during the nighttime hours (K. Simonsen, personal observation). When observed at the surface, bonito were also observed in the echograms making large vertical movements in the water column down to approximately 40 m depth, presumably to forage on vertically migrating prey. Bonito are opportunistic feeders, consuming crustaceans, small pelagic fishes, squid, fish larvae, and tunicates (Brooks, 2002). Even with the high MVBS in the surface water throughout the day, there was a more consistent diel pattern observed at the toppled platforms, suggesting that the light field around standing platforms may have an effect on behavior of the associated fish community.

Observed diel periodicity further elucidated the trends in pattern of MVBS, indicating a strong diel signal at both habitats and depths. These results are consistent with Peabody (2004), McDonough (2009), and Luo et al. (2009), who found strong diel periodicity in the movement of acoustically tagged fish around a standing platform and mangrove habitats, respectively. Equally telling was the lack of a distinct diel periodicity within 100 m of the standing platforms. While MVBS

was highly variable throughout the day, the diel cycle was the strongest signal, and it is unclear what these other peaks represent, as they are not consistent with depth, distance, and habitat. It may be that the 48-hour sample time at each habitat was not enough to reveal further periodicity than the diel signal observed. Tides, currents, or some other environmental factors may explain the remaining variability. Further sampling would be needed to determine the source of this variability.

The results of this study suggest that the light field around standing oil and gas platforms may have a significant effect on the behavior of the associated fish community. Though this study was limited to a small geographic area, the results are supported by the studies conducted by Peabody (2004) and McDonough (2009), though these were both limited to standing platforms, and unfortunately no such information exists on the movement of tagged fishes around toppled platforms. Very little information exists on the associated of fishes with toppled platforms in general (though see Wilson et al. 2003). Based on the results of the current study, it would be an interesting comparison to examine the movement of acoustically tagged fish around toppled oil and gas platforms, as no such information exists. This study does provide addition insight into how reef-associated fishes utilize large artificial reefs in the GOM.

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CHAPTER 3: HABITAT EFFECTS ON FEEDING ECOLOGY OF RED SNAPPER (*LUTJANUS CAMPECHANUS*): A COMPARISON BETWEEN ARTIFICIAL REEFS AND SHELF EDGE BANKS IN THE NORTHERN GULF OF MEXICO

Introduction

Red snapper (*Lutjanus campechanus*) is a long-lived, economically valuable finfish species found in abundance on the continental shelf throughout the Gulf of Mexico (GOM) and northwest Atlantic Ocean from Campeche, Mexico to Cape Hatteras, North Carolina (Wilson and Nieland 2001; Patterson et al. 2001b). Red snapper have pelagic larvae that settle out as juveniles on a variety of habitats, including sand, mud, and shell rubble (Szedlmeyer and Conti 1999; Patterson et al. 2005; Geary et al. 2007; Wells and Cowan 2007). As they mature, red snapper move to higher relief, more complex habitats, such as shell rubble, rocky reefs and artificial reefs of many types (Moseley 1966; Szedlmayer and Shipp 1994; Patterson et al. 2001a; Szedlmayer and Lee 2004; Wells et al. 2008b). Adult red snapper have been shown to exhibit a strong affinity for structure, and are often found abundantly around artificial reefs in the GOM (Szedlmeyer and Shipp 1994; Nieland and Wilson 2003; Patterson et al. 2005; Shipp and Bortone 2009; Cowan et al. 2011), including oil and gas platforms in the northwestern GOM (Wilson and Nieland 2001; Stanley and Wilson 2000, 2003). Despite this association, previous studies have demonstrated that the majority of prey items in the diets of red snapper are not reef associated, and instead are sourced from the surrounding water column and soft-bottom sediments (McCawley et al. 2006; McCawley and Cowan 2007; Wells et al. 2008a).

Red snapper are opportunistic feeders, consuming a variety of prey items, and exhibit an ontogenetic shift in their diets as they mature (Bradley and Bryan 1975; Szedlmayer and Lee 2004; Wells et al. 2008a). While juvenile red snapper consume primarily shrimp, squid, zooplankton, and other crustaceans (Bradley and Bryan 1975; McCawley et al. 2006; Wells et al. 2008a), adult red snapper are known to consume more fish and larger crustaceans including crabs and mantis shrimp (stomatopods) (Bradley and Bryan 1975; McCawley et al. 2006; Wells et al. 2008a). Despite the opportunistic feeding strategies of red snapper, previous studies have indicated that prey is sourced consistently from soft bottom sediments, regardless of the habitat on which they were collected (McCawley and Cowan 2007; Wells et al. 2008a), though some conflicting reports have suggested that a large portion of their diet does come from reef associated prey (Ouzts and Szedlmayer 2003; Szedlmayer and Lee 2004). This has caused extensive debate as to how artificial reefs function in the feeding ecology of red snapper.

Little information exists on the diets of red snapper from natural reefs, and from fish collected off the coast of Louisiana. This lack of information is surprising, given the high economic value of the species and the controversy concerning the management of the species (Cowan 2011; Cowan et al. 2011). Moseley (1965) provided one of the first studies of red snapper diet in the northern GOM. He reported diets of red snapper collected over natural habitat off the coast of Louisiana for both adults and juveniles. Adult red snapper were reported to consume a variety of prey items, including fish, squid, crabs, shrimp, mantis shrimp, and tunicates. Other studies in the northern Gulf of Mexico focused on natural and

artificial habitat in Texas (Bradley and Bryan, 1975; Davis 1975). Davis (1975) reported diets of red snapper to consist primarily of fish, squid, and crustaceans, such as crabs, shrimp, and mantis shrimp. Bradley and Bryan (1975) reported similar findings off the southern coast of Texas, indicating fish were the primary prey item, followed by crustaceans. The authors also reported that tunicates made up a significant portion of the diets during spring months. The majority of more recent studies on red snapper diet have taken place in Alabama on small artificial reefs (Outsz and Szedlmayer 2003; Szedlmayer and Lee 2004; McCawley et al. 2006; McCawley and Cowan 2007) and natural habitat (Wells et al. 2008a). Szedlmayer and Lee (2004) focused primarily on juvenile red snapper and found that younger fish fed primarily on fish and crustaceans, and that there were distinct shifts with habitat. Outsz and Szedlmayer (2003) examined adult red snapper, but found higher contributions of crustaceans to diets than previously reported. McCawley et al. (2006), McCawley and Cowan (2007), and Wells et al. (2008a) all found similar proportions of fish, squid, and crustaceans to previous studies.

The paucity of information available on red snapper collected from natural habitat is one of the key limitations in discerning the functional role of artificial reefs in the life history of red snapper. The majority of the early work was conducted before the stock was severely overexploited in the late 1980's (Cowan 2011). This is disconcerting given the largely discredited notion that a large "cryptic biomass" of red snapper exists over deeper shelf edge bank reefs in the northern GOM (Porch 2007; W. Mitchell, personal communication, NMFS, Beaufort, NC, USA). Whether or not a cryptic biomass does or does not exist, it is important to have an

understanding of how the various life history parameters (age and growth, diet, reproductive potential, etc.) of fish living on natural reefs, such as those on the shelf edge, compare to those found on inshore reefs or artificial structures.

Fish diets are best assessed using two different methods: gut content analysis and stable isotope analysis. Gut content analysis (GCA) is traditionally used to determine feeding habits of fishes because it provides an accurate description of recent feeding. GCA is not as useful for determining changes in feeding behavior, or describing feeding behavior over long time periods because of the relatively rapid depletion of stomach contents via digestion. Partially digested prey items are often hard to identify and may be underestimated when determining the overall contribution of prey to diet (Hyslop 1980; Grey et al. 2002; MacRae 2006). If large prey items are ingested, stomachs may contain only a limited number of prey, which may falsely indicate that the animal is a specialized feeder (Araujo et al. 2007). Additionally, prey is often patchily distributed and the source of prey can change over short intervals in time and space (Araujo et al. 2007). This, combined with opportunistic feeding by many fish species, can make gut content analysis an ineffective way to evaluate diets over long time periods. For these reasons, stable isotope analysis is often used in combination with GCA. Stable isotopes are used in ecological studies as indicators of feeding pathways over a longer time period, and have been used to determine feeding differences of organisms between habitats and among age classes (Fry, etc.). Compared to gut contents, stable isotope concentrations in fish tissue have a slow turnover rate, on the order of weeks to months for muscle tissue, and yield an integrated description of diet. The most

common isotope ratios used in studies of trophic ecology are $\delta^{13}\text{C}$ Carbon (C), $\delta^{15}\text{N}$ Nitrogen (N), and to a lesser degree $\delta^{34}\text{S}$ Sulfur (S), where $\delta^{13}\text{C}$ is most commonly used as an indication of the sources of primary production for the food web, $\delta^{15}\text{N}$ is an indication of trophic level, and $\delta^{34}\text{S}$ aids in differentiating feeding between salinity regimes, and therefore serves as an indicator of freshwater influence (Fry et al. 1999; Fry 2002; Wissel and Fry 2005). Stable isotope analyses are used increasingly more often in assessing marine food webs, though there are limitations to this technique. In diverse communities, such as those found in marine systems, there is considerable redundancy in types of organisms occupying the same trophic level. In such cases, diet variability can be underestimated based solely upon the $\delta^{15}\text{N}$ value of the predator and prey (Araujo et al. 2007). Conversely, some prey sources may be widely distributed, in which case isotopic analysis may show a greater variability in diet than actually exists (Araujo et al. 2007). For these reasons, stable isotope analysis is used most effectively in combination with GCA (Grey et al. 2002; Guiguer et al. 2002; Cocheret de la Moriniere et al. 2003; Lugendo et al. 2006; Wells et al. 2008a). Only a few studies in the GOM have used these two techniques in combination to assess fish diets from different habitat types (MacRae 2006; Wells et al. 2008a; Simonsen 2008; Wrest 2008).

Traditionally stable isotope analysis has focused on examining the mean values of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ for particular species in relation to some independent variable (site, habitat type, age, season, etc.) (Peterson et al. 1985; Deegan et al. 1990; Fry et al. 1999; Grey et al. 2002; Fry 2002; Wissel and Fry 2005). More recently techniques have been developed that take into account the variability of

stable isotope values both within the community and at the population level (Bearhop et al. 2004; Layman et al. 2007a, 2007b). These new approaches infer that greater variation in isotopic signatures for a population indicates a more complex food web, i.e. switching of diets, consumption of prey over a range of trophic levels, foraging over large spatial scales, or numerous sources of primary productivity in the food chain (Bearhop et al. 2004; Layman et al. 2007a, 2007b). Layman et al. (2007a) describe several different metrics for analyzing variation of niche space, as represented by a $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ biplot. These include $\delta^{13}\text{C}$ range, $\delta^{15}\text{N}$ range, total area (TA) of niche space, mean centroid distance for each point (CD), mean nearest neighbor distance, and standard deviation of nearest neighbor distance. Such metrics then can be used to describe the variation in feeding ecology of a single species (Layman et al. 2007b) or of the entire community (Layman et al. 2007a) over time, or between different habitat types, particularly if the potential sources of basal resources are also identified (De Mutsert 2010).

The objectives were to evaluate the habitat specific diets of red snapper; specifically, to contrast the dietary preferences of red snapper at associated with natural reefs along the shelf edge to large artificial reef habitats near the continental shelf edge of the northern GOM. This study sought to address a critical information gap regarding red snapper feeding ecology on from natural reef habitats. It was hypothesized that the diets on the natural reefs would be more diverse than diets at the artificial reefs, and therefore these fish would have a larger trophic niche breadth evident through stable isotope analysis. Finally, I wanted to determine if there were any prey items specific to the artificial reef habitats.

Methods and Materials

Red snapper were collected from eight different sites comprising three distinct habitat types, including two standing oil and gas platforms (hereafter standing), two oil and gas platforms that were cut and toppled in place to create artificial reefs (hereafter toppled) and four natural reefs (Figure 3.1). Only one red snapper with a useable stomach sample was collected from Rezak/Sidner bank (Figure 3.1), so this site was excluded from further analyses. Standing and toppled platform sites were located in the Eugene Island (EI) blocks in the northwestern Gulf of Mexico. Standing platform sites includes EI-346 and EI-325, both operational oil and gas platforms. Toppled platforms included EI-322 and EI-324, which were both toppled and converted to artificial reefs by the Louisiana Artificial Reef Program (LARP). Sampling was restricted to June and July during the summers of 2009 and 2010 to reduce the effects of seasonal bias thus concentrating on habitat differences.

Red snapper were collected with baited fish traps (hereafter traps), which were standard chevron (arrowhead) configuration, measuring 150 cm wide by 180 cm long by 60 cm high with an opening of 44.5 cm by 10 cm, and 3.8 mm wire mesh (Collins 1990; Wells et al. 2008b), and commercial fishing gear (hereafter fishing gear). Traps were set at each site at distances of 0.25, 0.5, 1.0, and 1.5 km in transects running north and south of the artificial structures (both toppled and standing) for a total of eight traps at each site. The time of day at which traps were set was random and varied by site and sampling trip both to avoid bias and to account for diurnal movement. Traps were baited and left to soak for two hours at

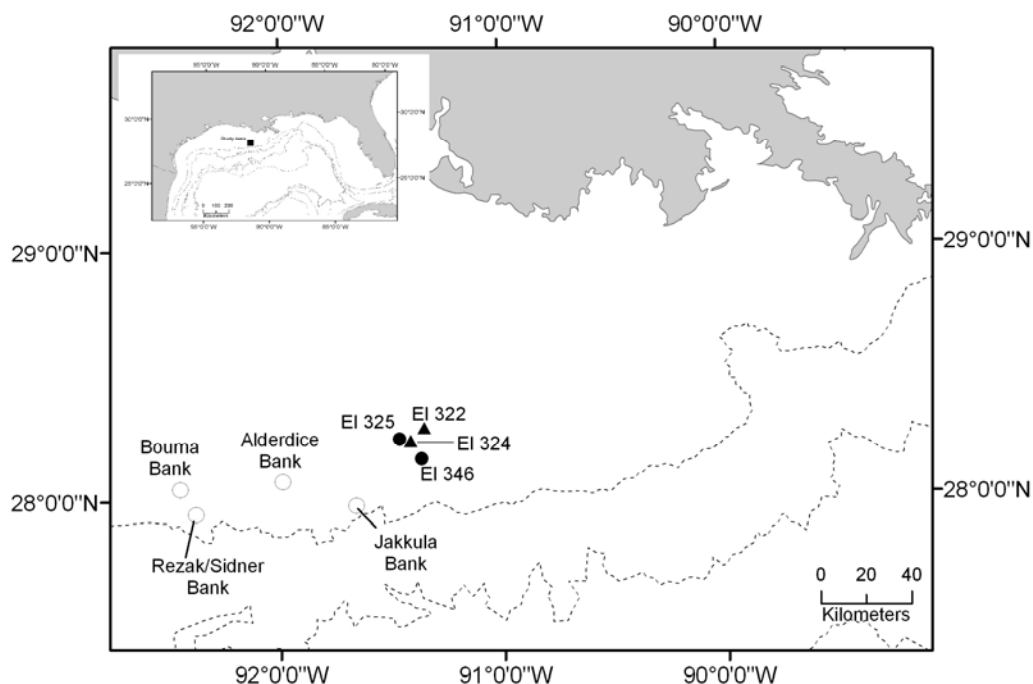


Figure 3.1: Location of red snapper (*Lutjanus campechanus*) sampling sites in the Gulf of Mexico. Open circles represent shelf edge bank (bank) sites. Closed circles represent standing oil and gas platform (standing) sites. Triangles represent toppled oil and gas platforms (toppled) sites. Dotted lines represent the continental shelf edge break.

each location. After soaking, the traps were recovered and all red snapper were numbered and placed on ice until processed on board the research vessel. Red snapper that were not processed at sea were kept on ice until return and analyzed in the laboratory. Fishing gear had four baited hooks and were fished for between one and two hours, until fifty fish were collected at each site, or as time and weather allowed. All other species were counted and discarded.

Stomachs of red snapper were removed and weighed to the nearest 0.1 g to determine full stomach wet weight, fixed in 10% formalin for 24 to 48 hours, and

subsequently transferred to ethanol for storage until analysis. Contents of the stomach and esophagus were removed, sorted under a dissecting microscope, and identified to the lowest taxonomic level possible. Stomach contents were then separated, grouped by taxon, and dried at 60°C for 24 to 48 hours in a drying oven. When possible, individual organisms were counted and recorded. Once dried, contents were weighed to 0.0001 g to determine dry weight of each taxonomic grouping of prey (hereafter prey items).

Stable isotope analysis was conducted on a sample of epaxial muscle tissue removed from the left flank, above the pectoral fin of each red snapper following the methods described in Zapp Sluis et al. (2013). Due to the large number of fishes collected, stable isotope analyses were limited to include only fish that had corresponding stomach samples, to permit assessment of the diets through the use of both techniques. Tissue samples were dried at 60°C for 24 hours in a drying oven and then pulverized. A sample of ground tissue weighing between 5.0 – 7.0 mg dry weight was placed in an aluminum capsule and mixed with approximately 10mg of vanadium pentoxide (V_2O_5). Samples then were analyzed for isotopic composition of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ with a Finningan MAT DeltaPlus® continuous-flow stable isotope mass spectrometer.

A sample of epaxial muscle tissue was also used to test for energy density to determine if the different habitats were contributing disproportionately to caloric intake of red snapper. Tissue samples were dried at 60°C for 24 hours in a drying oven and then pulverized, and subsequently pressed into a 1.0 g pellet for analysis.

Caloric density was determined with a Parr 6200® oxygen bomb calorimeter following McCawley and Cowan (2007).

Data Analysis

Three different methods were used to analyze the results of the gut content analyses, including percent composition by weight, percent composition by number, and frequency of occurrence. Percent composition by dry weight (%W) was used for the majority of statistical analyses because it is believed to provide the best assessment of the nutritional contribution of prey items (Bowen 1996; McCawley and Cowan 2007; Wells et al 2008a). As such, an index of relative importance (IRI) was constructed with the %W values for all prey items at each site with the formulas in McCawley and Cowan (2007). First, the frequency of occurrence (FO) was calculated as:

$$FO = \frac{\text{Number of stomachs containing one prey category}}{\text{Number of stomachs containing prey}}$$

The IRI is then calculated as:

$$IRI = (\%N + \%DW) \times FO$$

where N is the number each prey item found, DW is the total dry weight of each prey item and FO is the frequency of occurrence. Finally, a percent IRI (%IRI) is calculated as:

$$\%IRI = \frac{\text{IRI for each prey category}}{\text{Sum of all IRI values}} \times 100$$

The %IRI was used to examine the overall composition of red snapper diets at each habitat type (standing, toppled, and natural reef).

Gut content data were analyzed with PRIMER® (Plymouth Routine in Multivariate Ecological Research; Warwick, 1990) using percent composition by dry weight following a square root transformation to reduce heteroscedascity and to minimize the importance of abundant prey items. A Bray-Curtis similarity index was constructed from the transformed data, and a permutation analysis of variance (PERMANOVA) was run with this matrix to compare each stomach to every other stomach. A two-way PERMANOVA was used to compare prey items between habitat types and study years and *a posteriori* tests were applied. Following PERMANOVA, the original transformed data were analyzed with the similarity percentages (SIMPER) option, which examines within group (habitat) similarity as well as between group dissimilarity. This method allows the identification of prey items that contribute to differences in diets between habitats.

Caloric density data were compared among habitats, first with a two-way ANCOVA to test if total length was a significant covariate (SAS Institute, 2009). Following the ANCOVA, a two-way ANOVA was conducted to test for differences in caloric density between years and among habitats (SAS Institute, 2009). When necessary, Tukey HSD post ANOVA tests were applied for significant results at the $\alpha = 0.05$ level.

Stable isotope ratios were analyzed using both a multiple analysis of covariance (MANCOVA) to determine habitat specific differences in mean values of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$, and to compare trophic niche breadth between habitats

following Layman et al. (2007 a, b). A MANCOVA was performed on stable isotope data (SAS Institute, 2009), with fish total length (mm) as a covariate, for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$. Tukey post-hoc tests were applied to all tests with significant results at the $\alpha = 0.05$ level. For the trophic niche breadth analysis, all stable isotope values were first corrected for standard length using regression analysis. Adjusted values then were individually plotted as a $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ biplot to visualize niche space and make comparisons of dietary breadth among habitats using several different metrics, including total area (TA), centroid distance (CD), and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ range. TA is a measure of overall niche space that is determined by calculating the area associated with the smallest convex polygon that contains all individuals (Layman et al. 2007 a, b). CD is a measure of the overall trophic diversity that is determined by measuring the distance of each individual from the mean $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ value for the population (Layman et al. 2007 a, b). Mean centroid distances were compared among habitats using an ANOVA and Tukey HSD post ANOVA tests for significant results at the $\alpha = 0.05$ level. Calculation of TA and CD were completed with MATLAB (Mathworks, 2007, Massachusetts, USA). Range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are an indication of the overall range of basal resources and trophic diversity of the prey, respectively.

A complimentary study to this one (Terrebone-Daigle et al. 2013) collected potential sources of basal carbon from primary producers both in the water column and attached the standing platform structures. These sources include phytoplankton, red algae, green algae, and epiphytic algae. To determine which primary producers were incorporated into the diets of red snapper, a mixing model was constructed using IsoSource (Philips and Gregg 2003), which calculates the

range of all possible contributions from multiple sources (here primary producers) based on linear mixing models. The tolerance for the model was set at 0.01‰, which gives the most conservative estimate for the models. Only $\delta^{13}\text{C}$ was used in the IsoSource model because the differences in $\delta^{15}\text{N}$ among producers were not significant, and enrichment of $\delta^{15}\text{N}$ between trophic levels of producers and red snapper can skew the results. To account for trophic enrichment, values of $\delta^{13}\text{C}$ were adjusted based on trophic level of red snapper as determined from $\delta^{15}\text{N}$ values, following Terrebone-Daigle et al. (2013). Trophic level was determined using the formula:

$$\frac{\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{producer}}}{E} = \text{TL}$$

where $\delta^{15}\text{N}_{\text{consumer}}$ is the average delta value of the consumer (here red snapper) $\delta^{15}\text{N}_{\text{producer}}$ is the average delta value for potential primary producers, and E is the conservative enrichment estimate of ^{15}N per trophic level (3‰ used as a conservative estimate here). Mean values of $\delta^{13}\text{C}$ were adjusted by 0.5‰ per trophic level to account for trophic enrichment when running the model. Results are reported as the minimum, maximum (range) and mean value of contribution of each producer to the basal carbon source of red snapper.

Results

In total, 635 red snapper were collected in the summers of 2009 and 2010, of which 310 were used in the diet analysis. The remaining fish collected suffered from barotrauma, and had distended stomachs when brought on deck. Of the usable

stomachs sampled, 72 were collected from standing platforms, 58 were collected from toppled platforms, and 184 were collected from the natural reefs (Table 3.1).

Table 3.1: Number of useable red snapper stomachs sampled from each site during each year. Sites represent three distinct habitats, including standing oil and gas platforms (standing), toppled oil and gas platforms (toppled) and natural reef habitat in the Gulf of Mexico.

Habitat	Site	2009	2010	Total
Standing	EI-325	41	14	55
	EI-346	13	4	17
Toppled	EI-322	23	8	31
	EI-324	19	8	27
Natural Reef	Alderdice	18	20	38
	Bouma	70	0	70
	Jakkula	58	72	96

Diets of red snapper were significantly different among habitats, combined over years, based upon results of the PERMANOVA ($p < 0.05$). *A posteriori* tests revealed that diets of red snapper collected at toppled platforms were significantly different than those from both the standing platforms and the natural reefs. Diets were not significantly different between the standing platforms and the natural reefs ($p > 0.05$, PERMANOVA).

Overall, red snapper consumed primarily fish and crustaceans at all habitats and years, however the proportions were different between habitats (Figure 3.2). At the standing platform sites, diets were primarily fish, including antenna codlet (*Bregmaceros atlanticus*), squid, and unidentified crustaceans (hereafter

crustacean) by dry weight (Table 3.2; Appendix A), whereas at the toppled platforms, fish were common with the exception of antenna codlet (Table 3.2). Diets at toppled platforms consisted of more crustaceans, and unidentified crabs (hereafter crab), including bathyal swimming crab (*Bathynectes longispina*) (Table 3.2). Red snapper diets at the natural reefs were most varied, consisting mostly of fish including antenna codlet, and crab, including bathyal swimming crab (Table 3.2). There was also a significant contribution by colonial tunicates, likely the genus *Distalpia* spp. (hereafter tunicates), though very few tunicates were found in red snapper stomachs at the other two habitats, making up less than 1% at the standing platforms, and 0 found at the toppled platforms (Table 3.2).

The IRI generally agreed with diet analysis by dry weight at the standing platforms, indicating fish, squid and antenna codlet were the most significant contributors to diet (Table 3.2). At the toppled platforms, the results of the IRI differ from those of the analysis by dry weight. At these sites, stomachs contained a large number of benthic zooplankton, including amphipods, hyperid amphipods, *Cavalina* spp., and larval crabs. By weight, these prey items make up less than 1% of diets, but combine to contribute approximately 25% to diets of red snapper based upon the IRI (Table 3.2). Mantis shrimp (stomatopods), which were small, but numerous, and therefore not as important by dry weight, contributed another 9% to red snapper diets by IRI (Table 3.2). At the natural reef sites, the IRI generally agreed with the analysis by dry weight, and indicated that fish were the most important contributor to red snapper diets. The IRI differed with respect to tunicates, indicating less influence by this prey item than the analysis by dry weight. The

tunicates observed are colonial in nature, and therefore exist in the environment in dense groupings. Though found in the stomachs infrequently, when present, they were found in large masses in stomachs.

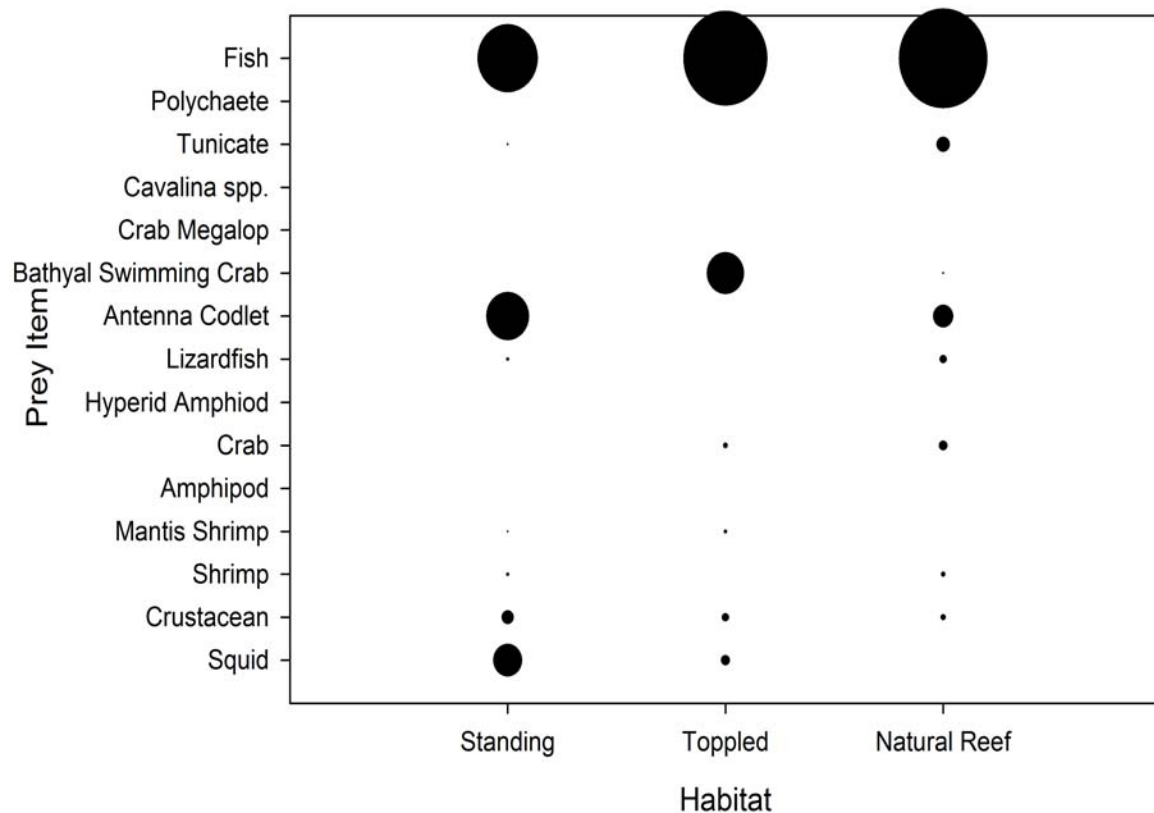


Figure 3.2: Diets of red snapper (*Lutjanus campechanus*) combined over summer 2009 and summer 2010 by percentage dry weight over three habitats in the Gulf of Mexico including standing oil and gas platforms (standing), toppled oil and gas platforms (toppled) and natural reef habitat. Samples are from red snapper collected in the summer of 2009 and 2010. Only the 15 most common prey items are displayed.

Table 3.2: Composition of red snapper (*Lutjanus campechanus*) diets, combined over years, by percentage dry weight (%DW) and Index of Relative Importance (IRI) at three different habitats, including standing oil and gas platforms (standing), toppled oil and gas platforms (toppled) and natural reefs.

Prey Item	Standing		Toppled		Natural Reefs	
	%DW	IRI	%DW	IRI	%DW	IRI
Unidentified	1.92		4.56		3.86	
Fish	39.83	55.47	55.95	39.19	59.18	68.66
Squid	18.61	8.50	5.34	2.62	0.27	0.14
Crustacean	7.56	6.01	4.36	12.28	2.67	4.91
Shrimp	1.36	0.73	0	0	2.22	2.33
Mantis Shrimp	0.43	1.02	1.79	9.11	0.13	0.40
Amphipod	0.03	1.45	0.03	5.34	0.05	2.51
Crab	0.39	0.01	2.56	0.39	5.16	8.72
Hyperid Amphiod	0.02	0.35	0.24	12.83	0.04	0.02
Lizardfish	1.37	0.08	0	0	4.24	0.18
Antenna Codlet	28.01	26.33	0	0	12.90	9.35
Bathyal Swimming Crab	0	0	24.49	6.53	0.49	0.01
Crab Larvae	0.01	0	0.29	4.11	0.07	0.10
<i>Cavalina</i> spp.	0	0	0.21	5.67	0.04	0.48
Polychaete	0	0	0.16	1.93	0.17	1.27
Tunicates	0.46	0.04	0	0	8.53	0.91

Diets of red snapper were also significantly different between years at all habitats. Several of the predominant prey items found in 2009 were absent in 2010, including antenna codlet and bathyal swimming crab. At the standing platforms, diets were similar between years, aside from the absence of antenna codlet. In 2009, antenna codlet, fish, squid, and crustaceans dominated diets (Table 3.3). In 2010, there were no antenna codlet and very few crustaceans found, with 76% of diets comprised of fish. Squid made up 18% of diets in both years. This pattern indicates a shift to more pelagic prey at the standing platforms. At the toppled platforms and the natural reefs, the shift was towards more benthic prey sources. In 2009, red snapper at the toppled platforms consumed mostly bathyal swimming

crabs, fish, squid, and crustaceans. In 2010, diets shifted to primarily fish and mantis shrimp (stomatopods), with a large percentage of unidentified material. At the natural reefs sites, diets shifted from fish, antenna codlet, and lizardfish in 2009 to fish and tunicates in 2010.

The IRI more clearly illustrates the differences between years. At the standing platform sites in 2009, the IRI indicates that fish, antenna codlet, crustaceans, and squid all contribute significantly to the diets, whereas in 2010 the diets are dominated by fish and squid (Table 3.4). At the toppled platforms sites, the diets shifted from hyperiid amphipods, fish, crustaceans, and crabs in 2009 to mantis shrimp, fish, amphipods, and *Cavallina* sp. in 2010. While there was some contribution from fish, the majority of prey items consisted of small, benthic invertebrates. At the natural reefs sites, the IRI indicates a shift from fish, including antenna codlet, in 2009 to lesser contributions of fish and more contribution from tunicates, and the associated invertebrate community. Found within the tunicate colonies were high numbers of amphipods, mantis shrimp, *Cavallina* spp., and polychaete worms, all of whom contributed more significantly to diets in 2010 based on the results of the IRI.

Mean caloric density was not different between habitats ($p > 0.05$, ANOVA), but was significantly higher in 2010 than in 2009 at all habitats ($p < 0.0001$, ANOVA). Length was not a significant covariate to caloric density ($p > 0.05$, ANCOVA), and therefore was analyzed using a two-way ANOVA to test differences. Mean caloric density values were generally higher at the standing platforms, though there were no significant differences between habitats.

Table 3.3: Percentage dry weight (%DW) of red snapper (*Lutjanus campechanus*) diets, by year at three different habitats, including standing oil and gas platforms (standing), toppled oil and gas platforms (toppled) and natural reefs.

Prey Item	Standing		Toppled		Natural Reef	
	2009	2010	2009	2010	2009	2010
Unidentified	1.56	3.11	4.08	30.22	3.11	4.02
Fish	28.84	75.78	44.17	35.94	52.06	67.13
Squid	18.73	18.21	7.30	0.44	0.33	0.14
Crustacean	9.81	0.21	5.99	0	3.37	0.76
Shrimp	1.57	0.67	0	0.07	3.18	0.39
Mantis Shrimp	0.55	0.05	0.61	25.56	0.03	0.28
Amphipod	0.05	0	0	0.55	0.02	0.10
Crab	0.51	0	3.52	0	5.94	3.42
Hyperid Amphiod	0.03	0	0.34	0	0.06	0
Lizardfish	1.79	0	0	0	6.51	0
Antenna Codlet	36.57	0.02	0	0	19.53	0.45
Bathyal Swimming Crab	0	0	33.62	0	0.75	0
Crab Megalop	0.01	0	0.38	0.28	0	0.20
<i>Cavalina</i> spp.	0	0.01	0	3.90	0	0.09
Polychaete	0	0	0	3.03	0	0.35
Tunicate	0	1.95	0	0	0	22.66

Table 3.4: Index of relative importance (IRI) of red snapper (*Lutjanus campechanus*) diets, by year at three different habitats, including standing oil and gas platforms (standing), toppled oil and gas platforms (toppled) and natural reefs.

Prey Item	Standing		Toppled		Natural Reef	
	2009	2010	2009	2010	2009	2010
Fish	45.21	78.36	27.63	15.25	85.59	59.94
Squid	7.56	17.32	3.56	0.10	0.04	0.17
Crustacean	8.15	0.45	22.18	0	2.65	0.41
Shrimp	0.77	0.92	0	0.01	2.35	0.52
Mantis Shrimp	0.75	1.72	1.16	49.65	0	2.13
Amphipod	1.84	0	0	12.97	0.03	12.46
Crab	0.02	0	0.54	0	0.10	1.58
Hyperid Amphiod	0.44	0	28.01	0	0.02	0
Lizardfish	0.12	0	0	0	0.12	0
Antenna Codlet	35.14	0.43	0	0	9.10	0.12
Bathyal Swimming Crab	0	0	8.36	0	0.01	0
Crab Megalop	0.01	0	8.54	0.08	0	0.78
<i>Cavalina</i> spp.	0	0.43	0	15.88	0	3.57
Polychaete	0	0	0	6.07	0	8.22
Tunicate	0	0.38	0	0	0	10.11

Table 3.5: Caloric density in cal/g for red snapper (*Lutjanus campechanus*) collected over three habitats including standing oil and gas platforms (standing), toppled oil and gas platforms (toppled) and natural reefs, in the northern Gulf of Mexico. Mean values, standard deviations (SD), and sample number (N) are shown.

Habitat	N	Mean Caloric Density (cal/g)	SD	N	Mean Caloric Density (cal/g)	SD
	2009			2010		
Standing	30	5365.22	157.63	15	5472.67	49.36
Toppled	19	5281.81	224.05	16	5522.52	61.39
Natural Reef	41	5356.11	163.80	20	5504.26	69.97

Stable Isotope Analysis

Overall, there were no consistent patterns in the stable isotope ratios of red snapper tissue. A significant enrichment of $\delta^{15}\text{N}$ ($p = 0.011$, ANCOVA) was observed at standing platforms, with post-hoc testing revealing the difference was based on enrichment at site EI-346. No other differences in $\delta^{15}\text{N}$ were observed among habitats (Figure 3.3). There were also differences with between years ($p < 0.0001$, ANCOVA), with samples from 2010 being more enriched in $\delta^{15}\text{N}$ than samples from 2009. There were no differences in ratios of either $\delta^{13}\text{C}$ or $\delta^{34}\text{S}$ of red snapper tissue samples either between years or among habitats ($p > 0.05$, ANCOVA).

As with the stable isotope analyses, there were few consistent patterns in the trophic niche breadth of red snapper. There were no significant differences in centroid distance (CD) among habitat types ($p > 0.05$, ANOVA), though there was a significant difference between years ($p < 0.001$, ANOVA), with 2010 having a significantly larger CD than 2009 among all habitats combined (Table 3.6). Post-hoc

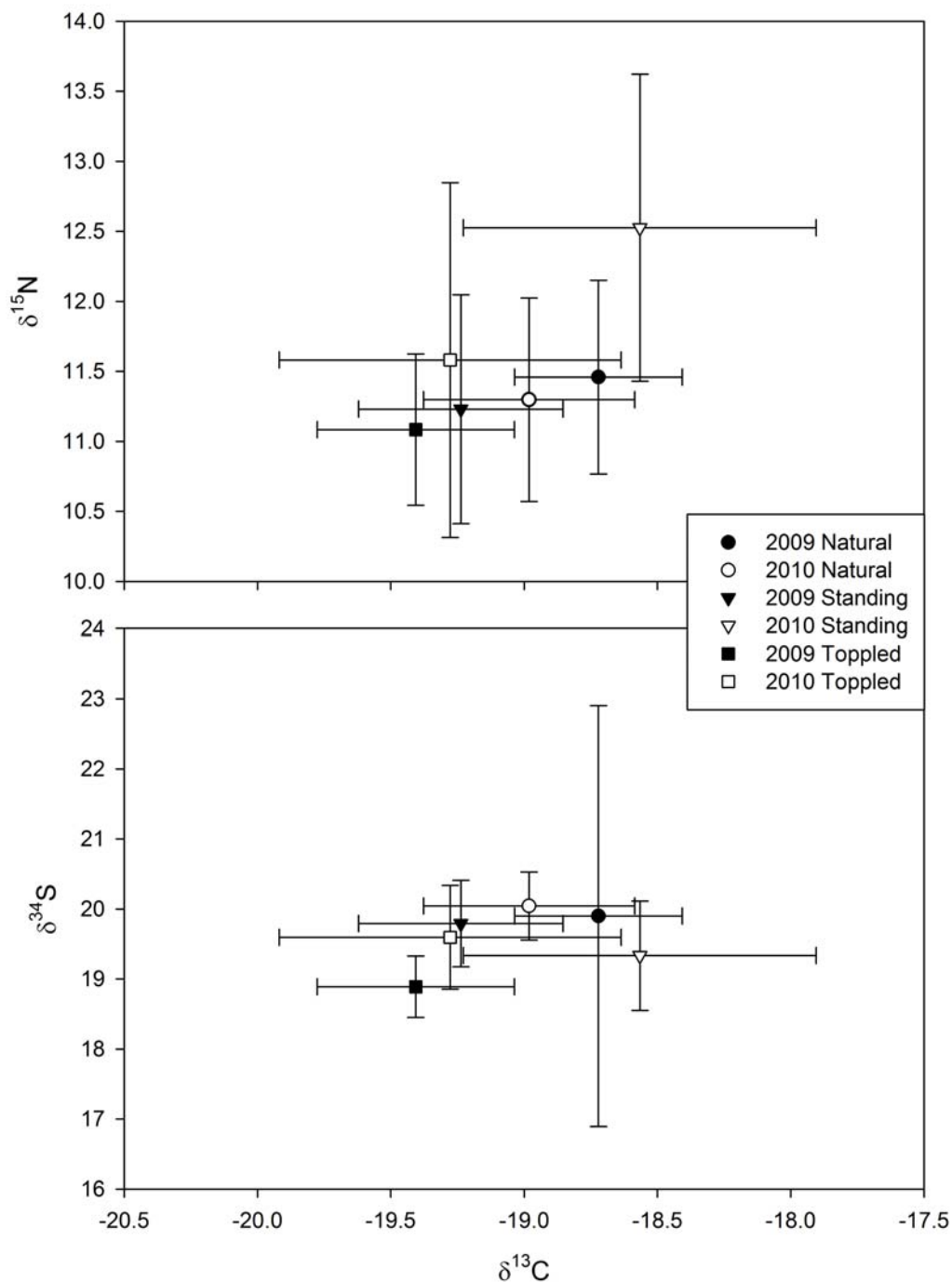


Figure 3.3: Mean stable isotope results values of red snapper (*Lutjanus campechanus*) as visualized by C-N (top) and C-S (bottom) biplots for three habitats in the Gulf of Mexico, including natural reefs (circle), standing platforms (standing; triangle), and toppled platforms (toppled; square). Standard error bars are shown around the mean. Years 2009 (closed symbol) and 2010 (open symbol) are represented separately due to observed differences between years at the standing platform sites.

testing indicated there was a higher CD in 2010 at both the standing and toppled platforms ($p = 0.0028$, ANOVA), with no differences in CD at the natural reefs between years. Total area (TA) of the C-N biplot of red snapper was approximately twice as large at the natural reefs as that of both standing and toppled platforms in 2009 (Figure 3.4; Table 3.6). In 2010, the TA was similar at standing and toppled platforms, both of which had a larger TA than the natural reefs (Table 3.6). Range of $\delta^{15}\text{N}$ was similar between all habitats during both 2009 and 2010, while $\delta^{13}\text{C}$ range was smaller at the toppled platforms, and similar between standing platforms and natural reefs (Table 3.6).

Table 3.6: Metrics for assessing trophic niche breadth of red snapper (*Lutjanus campechanus*) at three habitats, including standing oil and gas platforms (standing), toppled oil and gas platforms (toppled) and natural reefs in the northern Gulf of Mexico. Results are broken up by year. Values of total area of the C-N biplot (TA), centroid distance (CD) and range of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

Habitat	Year	TA	Mean CD	$\delta^{15}\text{N}$ Range		$\delta^{13}\text{C}$ Range	
				Low	High	Low	High
Natural Reef	2009	3.57	0.61 ± 0.45	11.17	16.03	-18.77	-16.60
	2010	1.50	0.66 ± 0.48	11.2	15.5	-18.4	-16.23
Standing	2009	1.98	0.66 ± 0.61	11.01	15.85	-18.62	-16.39
	2010	2.31	1.14 ± 0.52	11.53	15.68	-18.68	-16.12
Toppled	2009	1.51	0.52 ± 0.40	11.54	13.96	-18.78	-16.44
	2010	2.64	1.14 ± 0.79	11.35	15.74	-19.10	-16.57

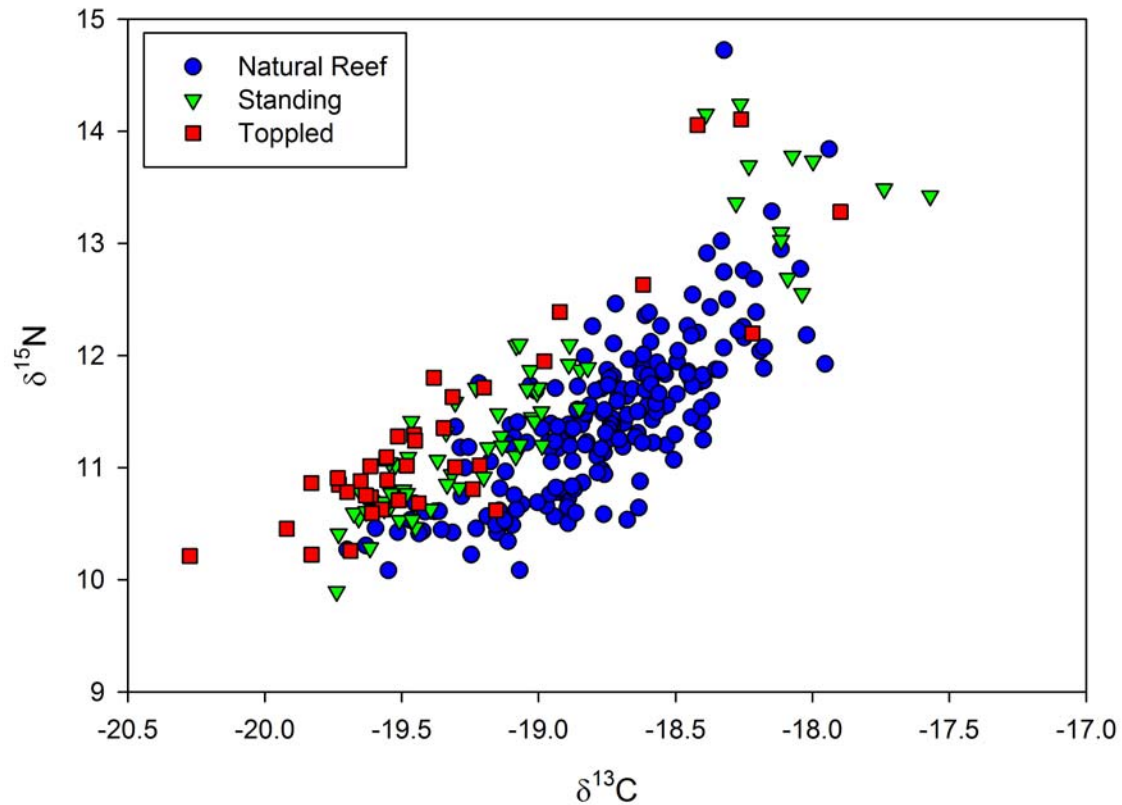


Figure 3.4: Stable isotope results from tissues samples of red snapper (*Lutjanus campechanus*) as represented by their carbon-nitrogen biplot. Data are length corrected and used to assess trophic niche breadth of three different habitats in the northern Gulf of Mexico including natural reefs (circle), standing oil and gas platforms (standing; triangle), and toppled oil and gas platforms (toppled; square).

Community Feeding Ecology

Results of the stable isotope analyses of red snapper were compared to stable isotope values of primary producers to determine if there were differences in basal carbon sources between habitats. Ranges of contribution for each primary producer were large, based on the results of the mixing model. Results indicate that phytoplankton and, to a lesser degree, epiphytic algae are the likely contributors of basal carbon to both the natural and artificial reef communities (Table 3.7). No differences were seen in the results between years, indicating that sources of basal

carbon remained consistent throughout the study period. Based on the fractionation rate of approximately 1‰ per trophic level, the most likely sources of basal carbon to the reef fish community are phytoplankton and epiphytic algae (Figure 3.5).

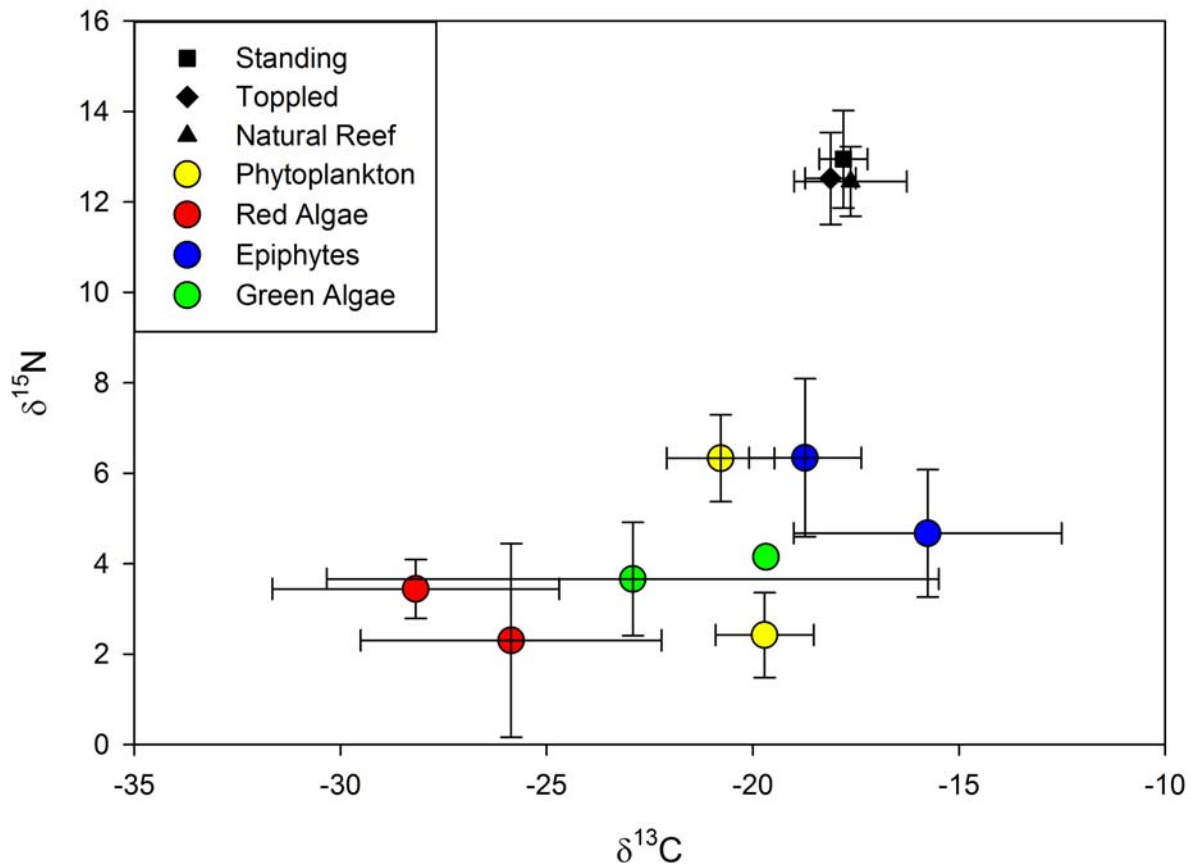


Figure 3.5: Mean stable isotope values of red snapper (*Lutjanus campechanus*) as visualized by the C-N biplot at three habitats in the northern Gulf of Mexico, including standing oil and gas platforms (standing; square), toppled oil and gas platforms (toppled; diamond) and natural reefs (triangle). Mean stable isotope values of basal resources (circle) including phytoplankton (yellow), red algae (red), epiphytes (blue) and green algae (green) are included for comparison. Solid circles represent samples from September 2010. Circles with crosshairs represent samples from April 2010. Isotope values of basal resources from Terrebone-Daigle et al. (2013). Standard error bars are shown around the mean.

Table 3.7: Results of the mixing models constructed in IsoSource to determine contribution of basal carbon sources to diets of red snapper (*Lutjanus campechanus*). Four potential basal resources are shown, based on results of Daigle et al. (2013). The minimum (min), maximum (max) and mean percentage composition are displayed.

Habitat	Year	Phytoplankton			Red Algae			Epiphytic Algae			Green Algae		
		Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean
Standing	2009	0	86	34	0	38	14	0	62	28	0	64	24
	2010	0	92	36	0	34	12	0	65	32	0	59	21
Toppled	2009	0	86	34	0	38	14	0	61	28	0	65	24
	2010	0	86	34	0	38	15	0	60	27	0	66	25
Natural Reef	2009	0	98	34	0	29	10	0	70	39	0	50	17
	2010	0	92	35	0	33	12	0	66	33	0	57	20

Discussion

Prior to this study the majority of the information available on red snapper feeding ecology came from studies conducted on artificial reefs (Cowan 2011; Cowan et al. 2010; W. Mitchell, personal communication, NMFS, Beaufort, NC, USA). Not only did this study add substantially to the red snapper diet data from natural habitats, it allowed for comparison of the feeding ecology of reef-associated species among artificial reefs and natural reefs located in similar depths. The natural reefs examined in this study were opportunistically selected because of their geographic proximity to the artificial reefs sampled, but it should be noted that these reefs are among the closest to the Mississippi River of the reefs on the continental shelf, and therefore are less complex than other reefs further west along the shelf (Merril et al. 1983; Gardner and Beaudoin 2005). Because of the complexity of the reefs to the west, the diets of reef-associated fishes may be much different than those collected in this study. Therefore, the results of this study do not reflect all the natural reefs along the Louisiana shelf edge, but do elucidate some of the similarities and differences in trophic ecology amongst habitats in the GOM.

While diets of red snapper were more diverse at the natural reefs than the other two habitats they consisted of prey items found at both other habitats. Overall, the diets of red snapper were more similar among habitats than expected. Those prey items that were found exclusively at any of the sites were found infrequently, making up less than 5% of total diets by dry weight, and therefore did not contribute significantly to the overall analysis. Additionally, the trophic niche breadth was not different between habitats, and no differences in nutritional

condition based on caloric density of red snapper tissue were observed. The reason for this may be due to trophic redundancy in diets over the natural reefs. The diets over the natural reefs also closely resembled the other two habitats, constituting prey items from both artificial reef sites. The overlap between diets at the natural reefs and the artificial reefs may be another reason no differences in niche breadth were observed.

Habitat specific differences in diets of red snapper were observed, however it is unclear whether or not these differences were due to distinct prey species associated with the habitats. The principle difference is in the proportion of fish and crustaceans present in stomachs of red snapper. A companion study to this one showed no discernible differences in the benthic invertebrate communities surrounding standing and toppled platforms (Terrebone-Daigle 2011). Therefore, it can be assumed that the prey base is the same around the two artificial reef habitats. Terrebone-Daigle (2011) used trawl samples to assess the benthic fish and invertebrate community structure and abundance around the artificial reef sites. However, only a few species collected in trawls appear in the diets of red snapper, and the most numerous prey item at the standing (antenna codlet) and toppled (bathyal swimming crab) platforms were both absent from trawl samples. The predominance of fish in the diets of red snapper at the standing platforms may be due to the vertical dimension of those structures. Standing platforms are complex vertical structures that extend throughout the water column and into the photic zone, which may aggregate fish species that become prey to red snapper. Another possibility is that small schooling fishes, such as antenna codlet, may be attracted to

the light from the standing platforms. Video observations of the standing platform sites indicated high numbers of antenna codlet around the standing platforms at night, when platforms were lit and lights were necessary on the ROV for visualization (K. Simonsen, personal observation). The standing platforms may aggregate prey in light field (Keenan et al. 2007), whereas the toppled platforms provide structure but no light field.

The higher $\delta^{15}\text{N}$ and higher caloric density (though not significant) observed in red snapper tissue samples at the standing platforms is consistent with the higher percentage of fish found in the diets at those sites. This trend follows a similar study by Zapp Sluis et al. (2013) who found that red snapper collected from platforms off the Louisiana coast were enriched in $\delta^{15}\text{N}$ as compared to fish collected on non-platform habitats. No differences in $\delta^{15}\text{N}$ were observed between toppled platform and natural reefs sites likely due to the higher amounts of crustaceans found and trophic redundancy of diets at the banks. There were no discernible differences in ratios of $\delta^{13}\text{C}$ or $\delta^{34}\text{S}$ in red snapper tissue between habitats or years, indicating consistent sources of primary production. This result, combined with the results of the mixing model, indicate that basal resources are the same throughout all habitats, and that prey are likely sourced from similar habitats, regardless of where the red snapper are collected. Comparisons with the stable isotope results from the complimentary study by Terrebone-Daigle et al. (2013) and a similar study by Zapp Sluis et al. (2013) confirm this finding. The mixing model and the values of $\delta^{13}\text{C}$ in red snapper tissue samples suggest that the basal carbon source is likely

phytoplankton and, to a lesser degree, epiphytic algae (Terrebone-Daigle et al. 2013).

Based on the components of the diet, the nutritional condition, and the stable isotope analysis, the diets of red snapper are similar among habitats and are consistently sourced from the surrounding water column and sea floor, as evidenced by phytoplankton serving as the basal carbon source (Terrebone-Daigle et al. 2013). Red snapper are known to be opportunistic in nature and feed on a wide variety of benthic invertebrates and demersal and pelagic fishes. Because diets of red snapper at the artificial reefs mimicked the diets of fish collected on nearby natural reefs, it is clear that red snapper in this area forage consistently along the seafloor and the surrounding water column, and very little of their diet is composed of reef-dependent organisms. There is ample evidence that red snapper make diel migrations away from the platform structures, presumably to feed (Peapody 2004; McDonough, 2009; Campbell et al. 2011). The results of this study support this finding, and are consistent with studies by McCawley and Cowan (2007), and Wells et al. (2008a). McCawley and Cowan (2007) found that only 1.6% of the diets of red snapper by dry weight consisted of reef-dependent organisms while the majority of the diets were sourced from surrounding soft-bottom sediments. Wells et al. (2008a) found that regardless of habitat type, red snapper prey was consistently sourced from sand and mud habitats.

Overall, I found no evidence of red snapper prey items specific to the artificial reef structures as compared to the natural habitat. Instead, certain prey items were absent from each of the artificial reef habitats that were found on the

natural bank sites. Therefore, the observed high biomass of red snapper around large artificial reefs in the northern GOM is likely due to factors other than site-specific prey availability. The large artificial reefs likely act as refuge from predation, and may act as buffers for high currents, making them an energy-efficient structure to inhabit. More recent information (Cowan et al. 2011) suggests that standing platforms may increase both fishing and predation mortality of red snapper because they are both easily located by anglers and concentrate large piscivores in the top 30 m of the water column (see Chapter 1; K. Simonsen, unpublished data). Another possibility is that large artificial reefs act as an intermediate habitat for large juvenile and young adult red snapper that are transitioning from inshore lower relief habitats, to offshore deeper water reefs (Nieland and Wilson 2003). This idea is supported by the fact that the majority (over 90%) of red snapper found around large artificial reefs are between 2 and 6 years old, and almost no older fish (> age 10) are found around these habitats (Nieland and Wilson 2003; Fischer et al. 2004, Saari 2011).

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CHAPTER 4: SPATIAL AND TEMPORAL TRENDS IN THE TROPHIC ECOLOGY OF REEF-ASSOCIATED FISHES AROUND STANDING AND TOPPLED OIL AND GAS PLATFORMS: EVIDENCE OF A FEEDING HALO?

Introduction

The northern Gulf of Mexico (GOM) is home to approximately 3000 oil and gas platforms, creating the largest *de facto* artificial reef deployment area in the world. The first oil platform in the GOM was installed in 1947, and since that time over 6500 have been constructed; however nearly 4000 have now been decommissioned and removed as leases in the GOM are terminated (Dauterive, 2000). While the main function of these structures is the production of oil and gas, they also increase in the amount of hard substrate present in the GOM, the majority of which are in areas that lack hard bottom substrate (Scarborough-Bull et al. 2008).

This addition of hard substrate provides additional habitat for the attachment of many sessile invertebrates and macroalgae (Scarborough-Bull and Kendall 1994; Scarborough-Bull et al. 2008), which in turn supports a diverse community, differing greatly from that found on the surrounding soft-bottom habitats. In this sense, it is estimated that the presence of oil and gas platforms has increased the overall biomass in the GOM at least for nonharvested species of fishes, invertebrates, and macroalgae (Scarborough-Bull et al. 2008). It was quickly realized that these large structures also attracted fishes, and supported a healthy community of reef-associated fishes, providing easy access for recreational and commercial fishers, as well as SCUBA divers. The accessibility of oil and gas platforms for fishing and other recreation led to the establishment of the Rigs-to-Reefs Program in the GOM (Kaiser, 2006). Bureau of Ocean Energy Management

(BOEM) rules state that a platform must be decommissioned within one year of the termination of a lease in the GOM (Dauterive 2000; Kaiser 2006). BOEM allows the transfer of a lease to a state sponsored program that then becomes responsible for the maintenance of the structure as an artificial reef.

Artificial reef programs are in place throughout the United States. In most cases, the reef programs are monitored by state government agencies, or not at all. Materials designated for reef building may be derived commercially, such as reef balls, or from “materials of convenience”, which can include anything from sunken vessels to subway cars. In Louisiana, the artificial reef program relies almost exclusively on material from decommissioned oil and gas platforms (Kaiser, 2006). There had been a push for use of decommissioned platforms to be turned into artificial reefs, due to the economic benefits to the energy companies involved, especially for large or complex rigs, and those in deep water, which are more expensive to remove (Kaiser, 2006). Therefore, a number of artificial reef planning areas have been set up, based on a set of criteria determined by BOEM (Dauterive, 2000). To date, over 300 structures comprising 67 sites have been turned into artificial reefs in nine planning areas that exist in the GOM (Wilson and Van Sickle 1987).

Despite the support for rigs-to-reefs programs in the GOM and deployment of artificial reefs in general, there has been much debate about how artificial reefs have affected the community of reef-associated fishes dwelling in the northern GOM. These questions focus mostly on the benefits, function, impact on fisheries, and implication for fisheries management associated with the addition of structure to

the GOM (Bohnsack et al. 1994; Strelcheck et al., 2005). The question of benefits of artificial reefs may therefore be thought of in terms of energetics. Fish consume prey, which in turn provides energy for basic life functions of growth, metabolism, reproduction, etc. The more prey available, presumably the higher the potential growth rate and production in this sense will not be the addition of new fishes to the system, but the enhanced growth (additional biomass) of those that already exist (Peterson et al. 2003; Powers et al., 2003; but see Lindberg et al. 2008; Cowan et al. 2011; Beisinger et al. 2011). From a bioenergetics standpoint, growth is a factor of prey consumption, minus the cost of metabolic processes and mortality, both natural and fishing (Kitchell et al. 1977). Therefore, whatever energy is provided by additional prey sources needs to outweigh the energetic costs of finding them (foraging migrations and prey capture) and the risk of predation associated with that habitat (predator avoidance and mortality). More specifically, if a large fish biomass associates with one structure, the prey resources may become locally depleted, resulting in a zone of prey depletion, or feeding “halo”, associated with the structure (Fraser and Lindberg 1994; Lindberg et al. 2006). As this feeding halo expands, the energy required to find and consume prey increases, as does the risk of predation (Fraser and Lindberg 1994; Biesinger et al., 2011). Fraser and Lindberg (1994) found that the abundance of soft-bottom prey increased with distance from constructed artificial reefs. Because of this, it has been hypothesized that each reef will have an area of prey depletion surrounding it, known as a “feeding halo”. If indeed a reef structure has an associated “halo” of prey depletion, then the available resources are a product of the size of the halo and reef spacing. Reefs that

are close together will have halos that overlap, resulting in overall decrease in available resources for those occupants of the reef conglomerate. This function may also be species specific, depending on size, swimming ability, habitat affinity, and home range of each species. For large mobile reef fishes, there may be some critical density of reefs that achieves maximum productivity (Shipley and Cowan 2010). This may be a function of reef size and spacing. Foraging excursions are energy and predation trade-offs. To be ecologically profitable, the amount of energy derived from feeding in the face of increased vulnerability to predation must be more than the energy used to make the foraging excursions (Werner et al. 1983; Biesinger et al. 2011). As prey is depleted near the structure, foraging excursions become longer. Depending on spacing, it may be energetically more efficient to move on to the next reef than return to the original reef at the end of a foraging route. Therefore, to effectively manage artificial reefs as reef fish habitat, this relationship between reef size, spacing, and food availability must be better understood (Fraser and Lindberg, 1994; Shipley and Cowan, 2010; Campbell et al. 2011). It is the focus of the current study to further the understanding of the relationship between reef fish biomass and trophic dynamics around large artificial reefs, including standing and toppled oil and gas platforms.

The objective of chapter 4 was to compare the trophic ecology of reef associated fishes, such as red snapper (*Lutjanus campechanus*) and rock sea bass (*Centropristis philadelphica*) among standing oil and gas platforms and previously decommissioned (toppled) oil and gas platforms. Specifically, I wanted to determine if there are differences in diets and basal resources between the two

structures, and determine if there are differences over seasons. Furthermore, I wanted to determine if a feeding halo was present around the large artificial reefs, and if so, what was the extent of such a feeding halo. If a feeding halo does exist, I wanted to examine whether the extent of this halo differed between standing and toppled platforms.

Methods and Materials

Reef-associated fishes were collected from four sites including two standing oil and gas platforms (hereafter standing), two oil and gas platforms that were cut and toppled in place to create artificial reefs (hereafter toppled). All four sites were located in the Eugene Island (EI) block of the Louisiana coast in the GOM (Figure 4.1). Standing platforms included EI 325 and EI 346, and toppled platforms included EI 322 and EI 324. Sampling was conducted quarterly from November 2008 through August 2010 to examine both habitat and seasonal effects on reef fish diets.

Two species of reef-associated fishes were collected for this analysis: red snapper, *Lutjanus campechanus*, and rock sea bass, *Centropristis philadelphica*. These species were chosen because they were among the most commonly and consistently collected during the study period, and are well suited to represent the trophic ecology of the demersal fish community in general. Red snapper were collected with baited fish traps (hereafter traps) and vertical longlines (hereafter longline). Rock sea bass were collected solely in traps. Traps were standard MARMAP chevron (arrowhead) configuration; measuring 150 cm wide by 180 cm

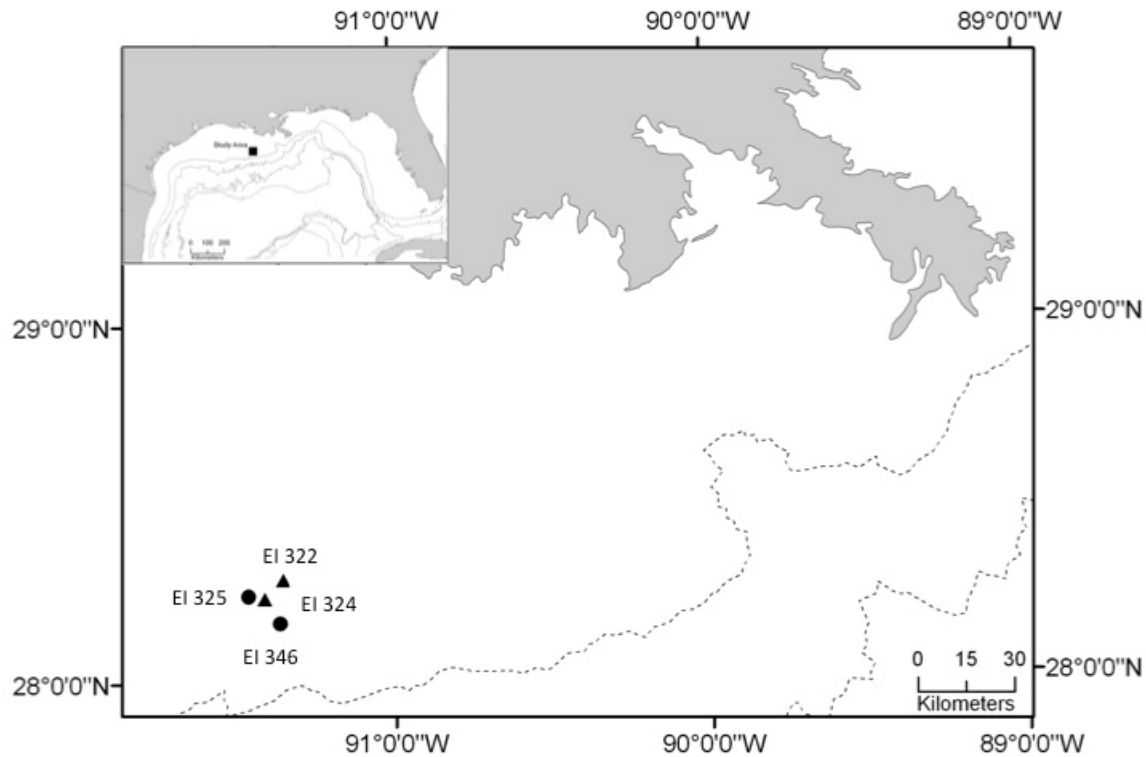


Figure 4.1: Sampling locations for reef fishes in the Eugene Island (EI) block of the northern Gulf of Mexico. Sites include two standing (circles) and two toppled (triangles) oil and gas platforms.

long by 60 cm high with an opening of 44.5 cm by 10 cm, and 3.8 mm wire mesh. Traps were set at each site at distances of 0.25, 0.5, 1.0, and 1.5 km in a transect running north to south for a total of eight traps at each site. The time of day at which traps were set varied haphazardly by site and sampling trip to avoid bias and to account for diurnal movement. Traps were baited and left to soak for two hours at each location. After soaking, the traps were recovered and all fishes were removed. Red snapper were numbered and placed on ice until processed on board the research vessel or until returned to the laboratory, as time allowed. Rock sea bass were counted, bagged by trap location, frozen, and returned to the laboratory where they were processed in the same manner as the red snapper. All other fishes

were counted, bagged, and frozen for analysis in the laboratory. Longlines had four baited hooks and were fished for between one and two hours, until fifty red snapper were collected at each site, or as time and weather allowed. All other species were counted and discarded.

Stomachs of red snapper and rock sea bass were removed and weighed to the nearest 0.1g to determine full stomach wet weight, fixed in 10% formalin for 24 to 48 hrs and subsequently transferred to ethanol for storage until analysis. Contents of the stomach and esophagus were removed, sorted under a dissecting microscope, and identified to the lowest taxonomic level possible. Stomach contents were then separated, grouped by taxon, and dried at 60°C for 24 to 48 hrs in a drying oven. When possible, individual organisms were counted and recorded. Once dried, contents were weighed to 0.0001g to determine dry weight of each taxonomic grouping of prey (hereafter prey items).

Stable isotope analysis was conducted on a sample of epaxial muscle tissue removed from the left flank of each specimen following Zapp Sluis et al. (2013). Due to the large sample sizes for both species, a subsample of fish was used for stable isotope analysis. For red snapper, stable isotope samples were limited to include only those fish that had corresponding stomach samples in order to make a broader assessment of the diets through the use of both techniques. For rock sea bass, those fish that had useable guts (not distended due to baurotrauma) were sampled first, and then randomly for those with distended stomachs, until a maximum of five were sampled from each trap (distance x site combination). Tissue samples were dried at 60°C for 24 hrs in a drying oven and then pulverized. A sample of ground tissue

weighing between 5.0 – 7.0 mg dry weight was placed in an aluminum capsule and mixed with approximately 10 mg of vanadium pentoxide (V_2O_5). Samples then were analyzed for isotopic composition of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ with a Finningan MAT DeltaPlus® continuous-flow stable isotope mass spectrometer.

A sample of red snapper muscle tissue was also used to test for energy density to determine if the habitats were contributing disproportionately to caloric intake of red snapper, and to examine seasonally variability of nutritional condition. Caloric density analysis was limited to red snapper only due to the small sample size of tissue collected from rock sea bass. Tissue samples were dried at 60°C for 24 hrs in a DX 600 drying oven and then pulverized, and subsequently pressed into a 1 g pellet for analysis. Caloric density was determined with a Parr 6200® oxygen bomb calorimeter.

Data Analysis

Gut content data were analyzed with PRIMER v.6 (Plymouth Routine in Multivariate Ecological Research; Warwick, 1990), using composition by dry weight following a square root transformation to normalize the data, and reduce the importance of abundant prey items. Because too few red snapper were caught in the traps at distances from the platform, gut content data was only compared between habitats and among seasons. For rock sea bass, data were compared between habitats, among seasons and with distance from the structure. A Bray-Curtis similarity index was constructed from the transformed data, and a two-way analysis of similarity (ANOSIM) was run to assess differences between habitats,

seasons, and distances (for rock sea bass). Following the ANOSIM, a permutational analysis of variance (PERMANOVA) was run, which not only examines the main effects, but the interaction between variables. A two-way PERMANOVA was used to compare the diets between habitat, season, and distance (for rock seas bass) and *a posteriori* tests were applied to the interaction terms. PERMANOVA is a useful and powerful tool to assess differences in groups of data, however it requires multiple samples to compare in order to maintain power in the analysis. Thus, ANOSIM was used to test for significant variables to use in the PERMANOVA model. Variables in the model are limited to maintain statistical power. Following PERMANOVA, the original square root transformed data was analyzed using the similarity percentages (SIMPER) option, which examines the within group (habitat, season, distance) similarity as well as the between group dissimilarity. This method allows the identification of prey items that contribute to the differences in diets between sites. Gut content data were further analyzed to incorporate both percent composition by number (%N) and frequency of occurrence (FO) with the percent composition by dry weight (%W), which gives a more robust interpretation of diets by incorporating small but numerically dominate prey items and decreasing the importance of large prey items (Bowen 1996; McCawley and Cowan 2007; Wells et al 2008a). As such, an index of relative importance (IRI) was constructed using the %W values for all prey items at each site with the formulas in McCawley and Cowan (2007). First the frequency of occurrence (FO) was calculated as:

$$FO = \frac{\text{Number of stomachs containing one prey category}}{\text{Number of stomachs containing prey}}$$

The IRI is then calculated as:

$$\text{IRI} = (\%N + \%DW) \times \text{FO}$$

where N is the number each prey item found, W is the total dry weight of each prey item and FO is the frequency of occurrence. Finally, a percent IRI (%IRI) is calculated as:

$$\% \text{IRI} = \frac{\text{IRI for each prey category}}{\text{Sum of all IRI values}} \times 100$$

The %IRI was used to examine the overall composition of diets for each species (red snapper and rock sea bass) at each habitat type (standing and toppled) by season and with distance from the reefs (for rock sea bass). Calculations for the IRI were completed in MATLAB (v 2007a, MathWorks, Nattick, MA USA).

Stable isotope data were assessed with a multiple analysis of covariance (MANCOVA) (SAS Institute, 2002), with fish total length as a covariate, to determine if there is a difference in mean values of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ for each species between habitat types, among seasons, and with distance from the sites. Following the MANCOVA, individual analyses of covariance (ANCOVA) are conducted for the dependent variables ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$). Values of stable isotope ratios also were used to analyze the niche breadth of each species at each site, following Layman et al. (2007 a, b). Samples were individually plotted in their $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ niche space for comparisons of dietary breadth between sites using two different metrics. Total area (TA) is a measure of overall niche space and is determined by calculating the area associated with the smallest convex polygon that contains all individuals (Layman et al., 2007 a, b). Centroid distance (CD) is a measure of the overall trophic diversity and is determined by recording the distance of each individual from the

mean $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ value for the population (Layman et al., 2007 a, b). Mean centroid distances were compared between sites using an ANOVA and Tukey HSD post ANOVA tests for significance at $\alpha = 0.05$ level. Calculation of TA and CD were completed using MATLAB (2007).

Caloric density data were compared among sites and seasons with a 2-way ANOVA and 2-way ANCOVA, with length as a covariate (SAS Institute, 2009). When necessary, Tukey HSD post ANOVA tests were applied for significance at $\alpha = 0.05$.

Acoustic Survey

Acoustic surveys were conducted during sampling trips to examine spatial distribution of fish biomass around structures (see Chapter 1 for a full description of sampling techniques). Acoustic backscatter data were collected using a BioSonics echosounder equipped with three downward-looking split-beam transducers (70, 120, and 200 kHz), calibrated by the standard sphere method (Foote et al. 1987). Data were collected at a threshold of -100 dB, with a pulse duration of 0.4 ms. Surveys were conducted at an average speed of 2 m s^{-1} and each transect was approximately 2 km in length, with the reef structure at the midpoint. Ten transects were completed at each site, conducted in a circular pattern, with each transect offset 18° from the previous line. Transducers were mounted on a pivoting boom that was lowered when on site, extending approximately 2 m depth below the surface to avoid bubbles entrained in the ships wake.

Acoustic backscatter data were post-processed using Echoview v. 5.3 (Myriax Pty. Ltd., Hobart, Tasmania, Australia) to obtain values of nautical area scattering

coefficient (NASC), an acoustic proxy for biomass (Simmonds and MacLennan 2005). Analysis thresholds were set in Echoview for Sv, and calibration settings were applied to compensate for the effects of temperature and salinity on speed of sound in seawater. A bottom detection algorithm with a 0.5 m backstep was applied to exclude the seafloor and reef structures from the analysis and then manually edited as needed (Ona and Mitson 1996).

NASC data were used to examine the spatial distribution of the potential prey base available to reef-associated fishes. After background noise removal, fish and zooplankton scatterers were separated into two echograms using the frequency response of the 120 kHz and 70 kHz frequencies through dB differencing, as described by Madureira et al (1993), Korneilussen and Ona (2002), Mosteiro et al. (2004), Korneilussen et al. (2009) and de Robertis et al. (2010). (See Chapter 1 for a full description). To examine the prey base, cleaned and processed echograms containing zooplankton scatters (fish biomass removed) were analyzed statistically using a mixed model to compare the effects of habitat, season, depth, and distance from the reef structure using NASC as the dependent variable. NASC is calculated from the mean volume backscattering strength (MVBS; Sv, expressed in dB), integrated over the depth layer of the sample, defined by spherical scattering and scaled to the nautical mile, and is understood to be proportional to the scattering biomass within the water column (MacLennan et al. 2002; Simmonds and MacLennan 2005). NASC was used here to serve as a measure of the prey distribution throughout the study area. Mean volume backscattering strength was linearized and compared between habitats, as a function of depth, and with hour of

the day using a mixed model (SAS v. 9.2, Cary, North Carolina, USA) with MVBS designated as the dependent variable in the model.

Results

Red Snapper

Red snapper were collected over eight sampling trips from November 2008 to October 2011. In total, 509 red snapper were collected from standing platforms, and 416 from toppled platforms for a total of 925 from all sites combined. Of the 925 red snapper collected, 408 had stomachs that were useable for gut content analysis, including 228 from standing platforms, and 180 from toppled platforms (Table 4.1). These included fish that did not have distended stomachs due to barotrauma, and ingested more than just bait. Overall, approximately 55% of the red snapper collected suffered barotrauma. Tissue samples were removed from all red snapper collected, however a subsample of 364 red snapper tissue samples were run for stable isotope analysis due to time and budget constraints. All samples used for stable isotope analysis also had a corresponding stomach sample to accompany the tissue sample. Using fish that could be analyzed in multiple ways provides a better overall view of the trophic ecology of red snapper. This included 218 from standing platforms and 135 from toppled platforms across all seasons (Table 4.1).

Table 4.1: Number of useable red snapper stomachs and tissue samples collected for diet analysis and stable isotope analysis, respectively. Sites represent two types of large artificial reefs in the Gulf of Mexico, including standing oil and gas platforms (standing) and toppled oil and gas platforms (toppled). Sites were in the Eugene Island (EI) blocks of the northern Gulf of Mexico.

Habitat	Site	2009		2010		Total	
		Stomachs	Tissue	Stomachs	Tissue	Stomachs	Tissue
Standing	EI-325	89	86	58	46	147	132
	EI-346	59	62	22	24	81	86
Toppled	EI-322	69	40	36	33	105	73
	EI-324	48	36	27	26	75	62

Diet Analysis

Results of the ANOSIM and PERMANOVA indicate there are significant differences in the diets of red snapper attributable to habitats and seasons. PERMANOVA also indicated there was a significant season x habitat interaction. Post-hoc testing indicated that diets were significantly different among seasons at the toppled platforms sites ($p < 0.05$, PERMANOVA). At the standing platform sites, diets differed significantly between fall and spring, fall and summer, winter and spring, and winter and summer. No differences existed between either fall and winter, or spring and summer at the standing platforms sites.

Overall, red snapper consumed primarily fish and crustaceans at all sites and seasons combined, though the proportions by dry weight were different, and varied by season (Figure 4.2). In the winter, red snapper consumed primarily

unidentifiable fish (hereafter fish) at both standing and toppled platforms. At the standing platforms, red snapper also consumed lizardfish (*Synodus* sp.), shrimp, squid, and some unidentified crustaceans (hereafter crustaceans) in the winter, while at the toppled platforms red snapper consumed crustaceans and unidentified crabs in the winter. In the spring, approximately 1/3 of red snapper diets consisted of fish, with a large amount of shrimp and squid at both standing and toppled platforms. At the standing platforms, antenna codlet (*Bregmaceros atlanticus*) were observed frequently in the stomachs of red snapper in the spring and summer, while no antennae codlet were found at toppled platforms. At the toppled platforms in the summer, red snapper consumed primarily crabs, particularly bathyal swimming crab (*Bathynectes longispina*). Fall diets were least variable during this study, and consisted almost exclusively of fish at the standing platforms, and squid and fish at the toppled platforms; low variability in diet may be owing to lower sample size in fall.

The IRI generally agreed with the results by dry weight, however there were differences based upon many of the prey categories that included small but numerically dominate taxa (Table 4.2). The IRI emphasizes these prey items, based upon both the numbers at which they were consumed. Conversely, many prey items that contributed by dry weight do not contribute as heavily to the IRI based on the low of frequency in guts and small numbers consumed. The IRI indicates that fish dominated the diets at the standing platforms in both the fall and winter, whereas the importance crustaceans was lower in the fall and the importance of lizardfish was higher in the winter based on the IRI. At toppled platforms in the fall and

winter, the importance of fish was lower based on the IRI, while the importance of and both crustaceans and squid was higher in the winter and fall. In the spring and summer samples, the analysis by dry weight and the IRI agree. There were several small, but numerically dominant prey items identified by the IRI, including crustaceans at both habitats in both the spring and summer, *Cavalina* sp. (Pteropoda) at the toppled platforms in both spring and summer, and crab larvae at the toppled platforms in the summer.

Table 4.2: Percentage index of relative importance (%IRI) of red snapper diets, by season, at two different habitats including standing oil and gas platforms (standing) and toppled oil and gas platforms (toppled). Data are combined over sampling years.

Prey Item	Winter		Spring		Summer		Fall	
	Standing	Toppled	Standing	Toppled	Standing	Toppled	Standing	Toppled
Fish	91.04	62.72	35.98	25.86	57.98	47.91	90.71	65.67
Crab	0.03	0.12	0.05	0	0.03	0.78	0	0
Mollusc	0	0	0.23	0.02	0	0	0	0
Shrimp	1.52	0.13	4.01	12.35	0.55	0.01	0.14	0
Squid	1.07	0.33	6.00	7.22	5.95	1.28	0.46	17.99
Crustacean	3.37	33.96	42.41	36.31	5.07	9.19	8.55	16.34
Mantis Shrimp	0.45	2.74	0.20	4.52	0.54	8.04	0.07	0
Amphipod	0	0	0.05	1.89	1.72	7.26	0	0
Hyperid								
Amphipod	0	0	0.02	4.69	0.20	10.89	0	0
Lizardfish	1.57	0	0	0.83	0.11	0	0	0
Antenna								
Codlet	0.79	0	10.53	0	27.48	0	0	0
Bathyal Swim								
Crab	0	0	0	0	0.00	2.65	0	0
Sponge	0.12	0	0	0	0.09	0	0	0
Crab Megalop	0.02	0	0	0.19	0	3.44	0	0
Worm	0	0	0	0	0	0	0	0
Cavalina	0	0	0.05	6.11	0.26	5.95	0.07	0
Polychaete	0	0	0.45	0	0.01	2.53	0	0

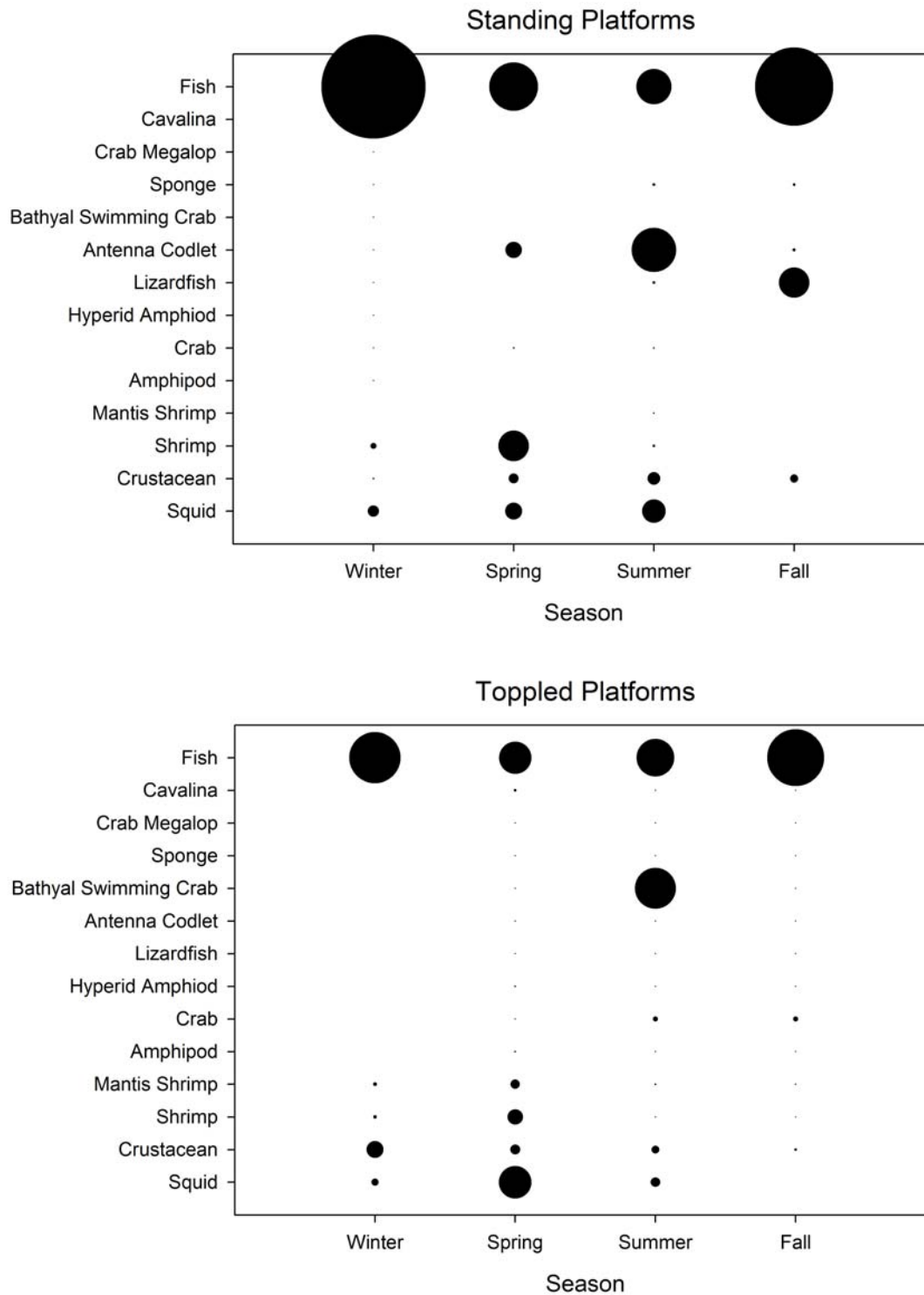


Figure 4.2: Diets of red snapper (*Lutjanus campechanus*) based on percentage dry weight, by season, at two different habitats including standing oil and gas platforms (standing) and toppled oil and gas platforms (toppled). Data are combined over sampling years.

Stable Isotope Analysis

Comparisons could not be made for red snapper with distance from sites, due to small catch totals away from the reef structure. Therefore, data were combined over distance to examine seasonal and habitat specific differences. Results of the MANCOVA indicate that length is a significant covariate for all of the dependent variables, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ ($p < 0.0001$, MANCOVA). There was significant enrichment of $\delta^{15}\text{N}$ ($p < 0.05$, MANCOVA) at the standing platform sites throughout the sampling period, with the exception of fall samples, when red snapper tissue was significantly more enriched at the toppled platform sites (Figure 4.3). Red snapper tissue was also significantly more enriched in $\delta^{15}\text{N}$ during the fall, while being more depleted in $\delta^{15}\text{N}$ during the summer. Ratios of $\delta^{13}\text{C}$ also differed with both habitat and season, with significant enrichment of $\delta^{13}\text{C}$ at the standing platform sites throughout the study period, ($p < 0.05$, MANCOVA), again with the exception of fall samples (Figure 4.3). Red snapper tissue was more enriched in $\delta^{13}\text{C}$ during the fall and was significantly more depleted ($p < 0.0001$, MANCOVA) in the summer months (Figure 4.3). No differences were seen in mean values of $\delta^{34}\text{S}$ either between habitats or amongst seasons ($p > 0.05$, MANCOVA).

Results of the trophic niche breadth analysis showed no significant difference in centroid distance (CD) between habitats (Table 4.3). There was, however a significant difference in CD among seasons ($p < 0.0001$, ANOVA), with a significantly larger CD in the summer than both the winter and spring at both habitats. The overall total area (TA) was similar between both habitats (Table 4.3), however the TA at the toppled platforms was more variable over seasons (Figure 4.4). In the fall,

the TA was roughly half that of the spring and summer months, and nearly 50% smaller in the winter (Figure 4.4). The TA at the standing platforms remained relatively constant throughout the year (Figure 4.4). The overall $\delta^{15}\text{N}$ range was larger at the standing platforms, while the overall $\delta^{13}\text{C}$ range was larger at the toppled platforms (Table 4.3). The range of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was larger in the summer and fall (Table 4.3).

Table 4.3: Metrics for assessing trophic niche breadth of red snapper (*Lutjanus campechanus*) at two habitat types in the Gulf of Mexico, including standing oil and gas platforms (standing) and toppled oil and gas platforms (toppled) habitat, by season, combined over years. Metrics of total area (TA), mean centroid distance (CD) \pm standard deviation, $\delta^{15}\text{N}$ range, and $\delta^{13}\text{C}$ range are shown.

Habitat	Season	TA	Mean CD	$\delta^{15}\text{N}$ Range		$\delta^{13}\text{C}$ Range	
				Low	High	Low	High
Standing	Overall	6.6812	1.01 \pm 0.63	10.51	15.35	-19.76	-17.42
	Winter	4.4534	0.79 \pm 0.64	10.82	15.31	-19.39	-17.42
	Spring	4.2074	0.78 \pm 0.62	11.57	15.35	-19.47	-17.71
	Summer	3.9604	1.22 \pm 0.58	10.52	15.30	-19.73	-17.57
	Fall	4.2848	1.00 \pm 0.63	10.53	15.18	-19.76	-17.69
Toppled	Overall	6.4915	0.99 \pm 0.59	10.56	15.02	-20.28	-17.40
	Winter	2.5115	0.90 \pm 0.58	10.56	14.25	-19.90	-17.99
	Spring	3.2985	0.90 \pm 0.54	10.86	13.96	-19.74	-17.52
	Summer	3.7371	1.10 \pm 0.58	10.64	15.02	-20.28	-17.90
	Fall	1.8706	0.94 \pm 0.93	11.69	14.86	-20.28	-17.40

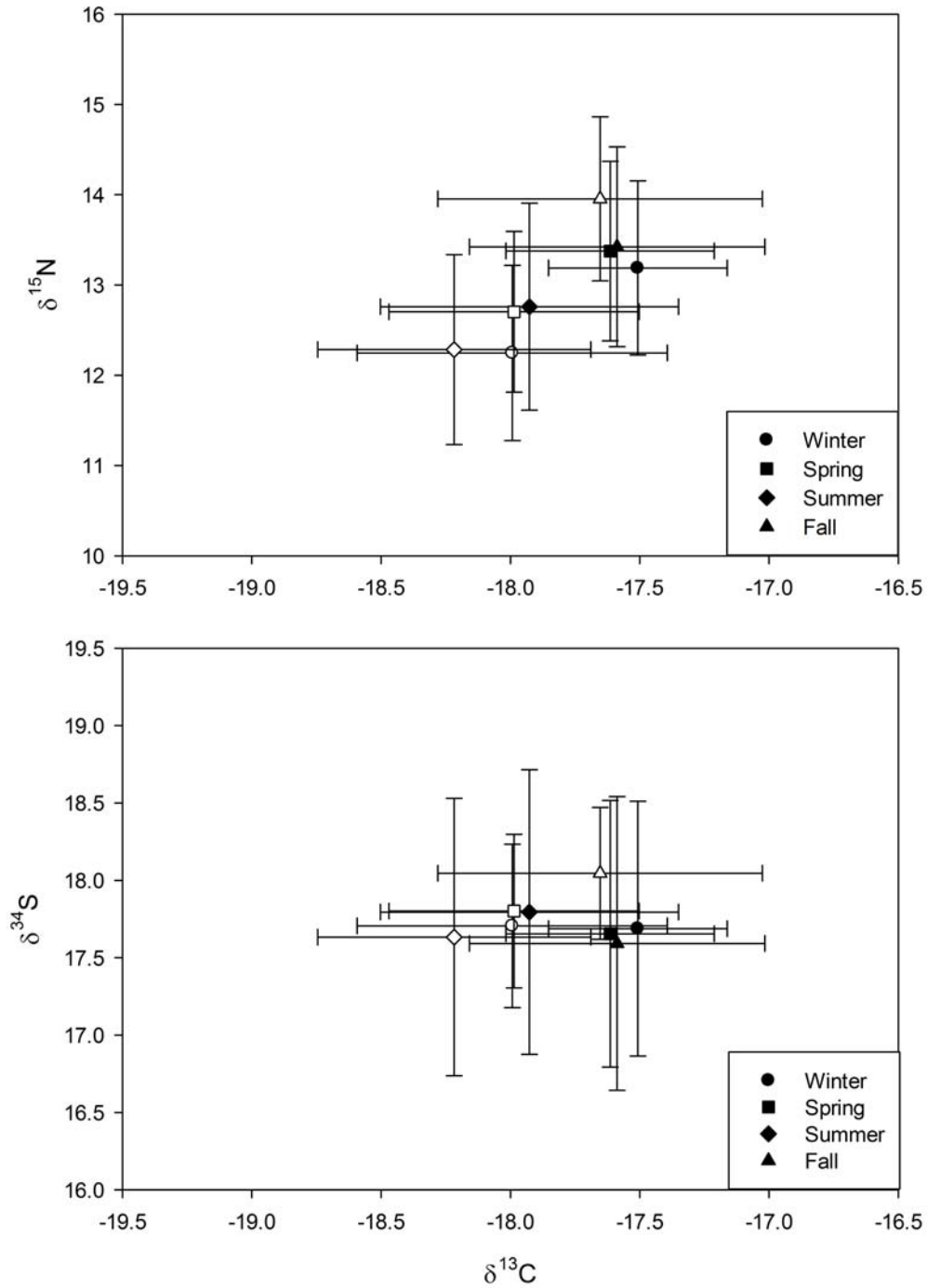


Figure 4.3: Mean stable isotope results values of red snapper (*Lutjanus campechanus*) as visualized by C-N (top) and C-S (bottom) biplots for two habitats in the Gulf of Mexico, including standing (closed symbols) and toppled (open symbols) oil and gas platforms. Results are combined over years and visualized over seasons as winter (circle), spring (square), summer (diamond) and fall (triangle). Standard error bars are shown around the mean.

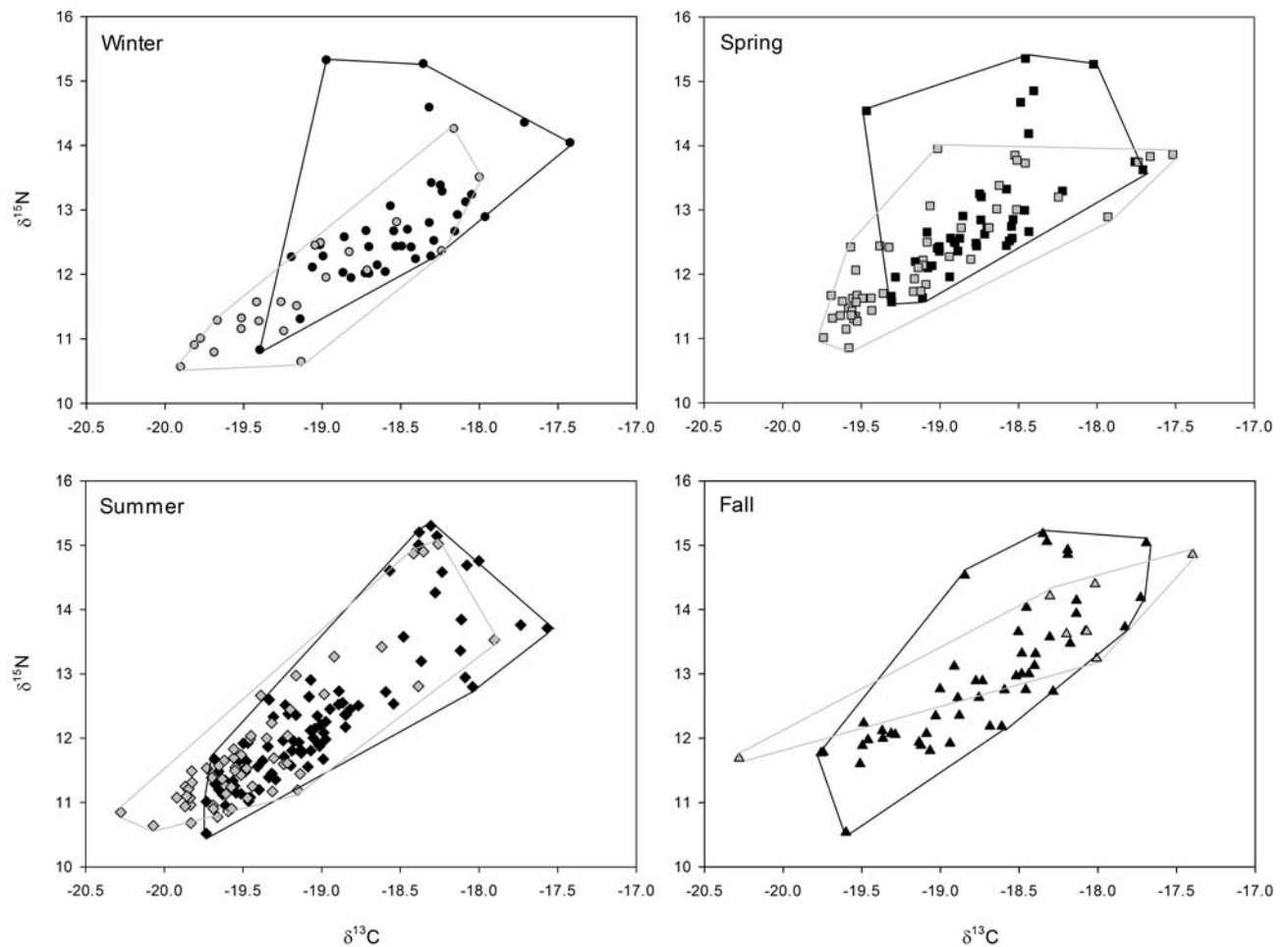


Figure 4.4: Stable isotope results from tissues samples of red snapper (*Lutjanus campechanus*) as represented by their carbon-nitrogen biplot. Data are length corrected and used to assess trophic niche breadth between two habitat types in the northern Gulf of Mexico including standing (black) and toppled (grey) oil and gas platforms. Total area (TA) of trophic niche as indicated by convex polygon displayed. Data are displayed separately for each season.

Caloric Density

Mean caloric density did not differ significantly between habitat types but did differ significantly among seasons (Table 4.4). Results of the ANCOVA indicate that caloric density did not covary with total length ($p > 0.05$, ANCOVA), and therefore the model was run as an ANOVA to determine differences in mean caloric

density between habitat types and among seasons. There was no difference in caloric density between years ($p > 0.05$, ANOVA), so data were combined over years in the model. Seasonal differences in mean caloric density were observed, with summer samples having significantly lower caloric density than spring samples (Table 4.4). Pairwise testing revealed no further differences between seasons, but did indicate that samples collected in the month of June had significantly lower caloric density than those collected in all other months.

Table 4.4: Caloric density (in cal/g) of red snapper (*Lutjanus campechanus*) at two habitat types in the Gulf of Mexico, including standing oil and gas platforms (standing) and toppled oil and gas platforms (toppled) habitat, by season, combined over years.

Season	Habitat	Caloric Density (cal/g)	Standard Deviation
Winter	Standing	5459.13	100.87
	Toppled	5426.52	158.64
Spring	Standing	5484.95	77.64
	Toppled	5467.08	68.31
Summer	Standing	5442.99	137.73
	Toppled	5402.95	168.55
Fall	Standing	5404.71	56.16
	Toppled	5468.01	73.78

Rock Sea Bass

A total of 341 rock sea bass were collected over eight sampling trips from November 2008 to October 2011, including 114 from toppled platforms, and 227 from standing platforms. The rate of barotrauma was higher in rock sea bass than red snapper, comprising nearly 80% of all fish collected, and therefore only a small

subsample was available for gut content analysis. In total, 77 rock sea bass, including 34 fish from toppled platforms, and 43 from standing platforms had useable stomachs for gut content analysis (Table 4.5).

Table 4.5: Number of viable rock sea bass stomachs and tissue samples collected for diet analysis and stable isotope analysis, respectively. Sites represent two types of large artificial reefs in the Gulf of Mexico, including standing oil and gas platforms (standing) and toppled oil and gas platforms (toppled). Sites were in the Eugene Island (EI) blocks of the northern Gulf of Mexico. Data combined over sampling years.

Habitat	Site	Collected	Samples	
			Stomachs	Tissue
Standing	EI-325	77	21	24
	EI-346	150	22	20
Toppled	EI-322	24	11	6
	EI-324	90	23	7

Diet Analysis

Due to the limitations of the ANOSIM and PERMANOVA analyses (see Methods) a series of tests were run to examine the effects of season, habitat, and distance on the diets of rock sea bass. Results of the ANOSIM and PERMANOVA indicate there are no significant differences in diets of rock sea bass between habitats. There were seasonal differences, and post-hoc testing showed that at the toppled platforms sites, diets were only significantly different between fall and winter. At the standing platform sites, summer diets differed significantly from

other seasons. Differences were also identified among distances from the platforms, and these results were dependent upon habitat. At the toppled platforms, diets were significantly different at a distance of 1.0 km than all other distances. At the standing platform sites, diets were significantly different between 0.5 km and both 0.25 km and 1.0 km. No other differences in diets with distance were observed. Furthermore, there were not enough viable samples to compare the variability with distance amongst seasons. Data comparing distances are therefore combined over seasons.

A smaller variety of prey items were found in the stomachs of rock sea bass than were found in red snapper, yet were also comprised mostly of fish and crustaceans. Diets also varied by season, with more variety found in the spring and summer (Figure 4.5). In the winter, rock sea bass consumed almost exclusively fish at both standing and toppled platforms. In the spring, rock sea bass consumed primarily fish, squid, tunicates and a variety of crustaceans at the standing platforms. At the toppled platforms in the spring, rock sea bass consumed primarily squid, with some contribution of fish and elbow crab (Parthenopidae). In the summer, rock sea bass again consumed primarily fish, specifically frogfish and lizardfish at the standing platforms. Diets of rock sea bass at the toppled platforms in the summer had low variety, likely due to low sample size, and included fish, crab, and unidentified material. In the fall, rock sea bass at both habitats consumed primarily fish and crustaceans, including longspine swimming crab (*Portunus spinicarpus*). The IRI again generally agreed with the results by %DW, indicating fish and crustaceans were most important to the diets of rock sea bass (Table 4.6).

Table 4.6: Percentage index of relative importance (%IRI) of rock sea bass (*Centropristis philadelphica*) diets, by season, at two different habitats including standing oil and gas platforms (standing) and toppled oil and gas platforms (toppled). Data are combined over sampling years.

Prey Items	Winter		Spring		Summer		Fall	
	Standing	Toppled	Standing	Toppled	Standing	Toppled	Standing	Toppled
Fish Tissue	96.25	76.48	26.82	26.31	73.25	50.78	50.61	69.59
Crustacean	0	14.79	14.41	2.86	6.04	0	0	16.83
Mysid	0	5.47	0	0	0	0	0	0
Tunicate	0	0	5.42	0	2.82	0	0	0
Mantis Shrimp	2.55	0	1.16	3.11	0.93	0	0	0
Squid	0	0	10.05	52.43	2.11	0	15.88	0
P. Shrimp	1.21	3.26	31.24	7.11	1.34	0	13.35	2.59
Amphipod	0	0	0	1.43	0	0	0	0
Crab	0	0	0.82	0	6.89	49.22	0	6.67
Sponge	0	0	1.06	0	0.70	0	0	0
Scallop	0	0	0.41	0	0	0	0	0
Elbow Crab	0	0	7.82	6.75	1.90	0	0	0
Longspine Sw. Crab	0	0	0	0	0	0	20.16	4.31
Tunicate (<i>Distalpia</i> sp.)	0	0	0.77	0	0	0	0	0
Frogfish	0	0	0	0	3.01	0	0	0
Lizardfish	0	0	0	0	1.01	0	0	0

Differences were identified in the diets of rock sea bass with distance from the structure. At standing platforms, diets were significantly different at 0.5 km than both .025 and 1.0 km. At 0.25 and 1.0 km rock sea bass consumed a larger variety of prey items than the other two distances (Figure 4.6), including fish, squid, elbow crab, and penaeid shrimp. At both 0.5 and 1.5 km, variety of diets was very low and consisted primarily of fish. At the toppled platforms, diets at 1.0 km were significantly different than all other distances, and consisted primarily of fish

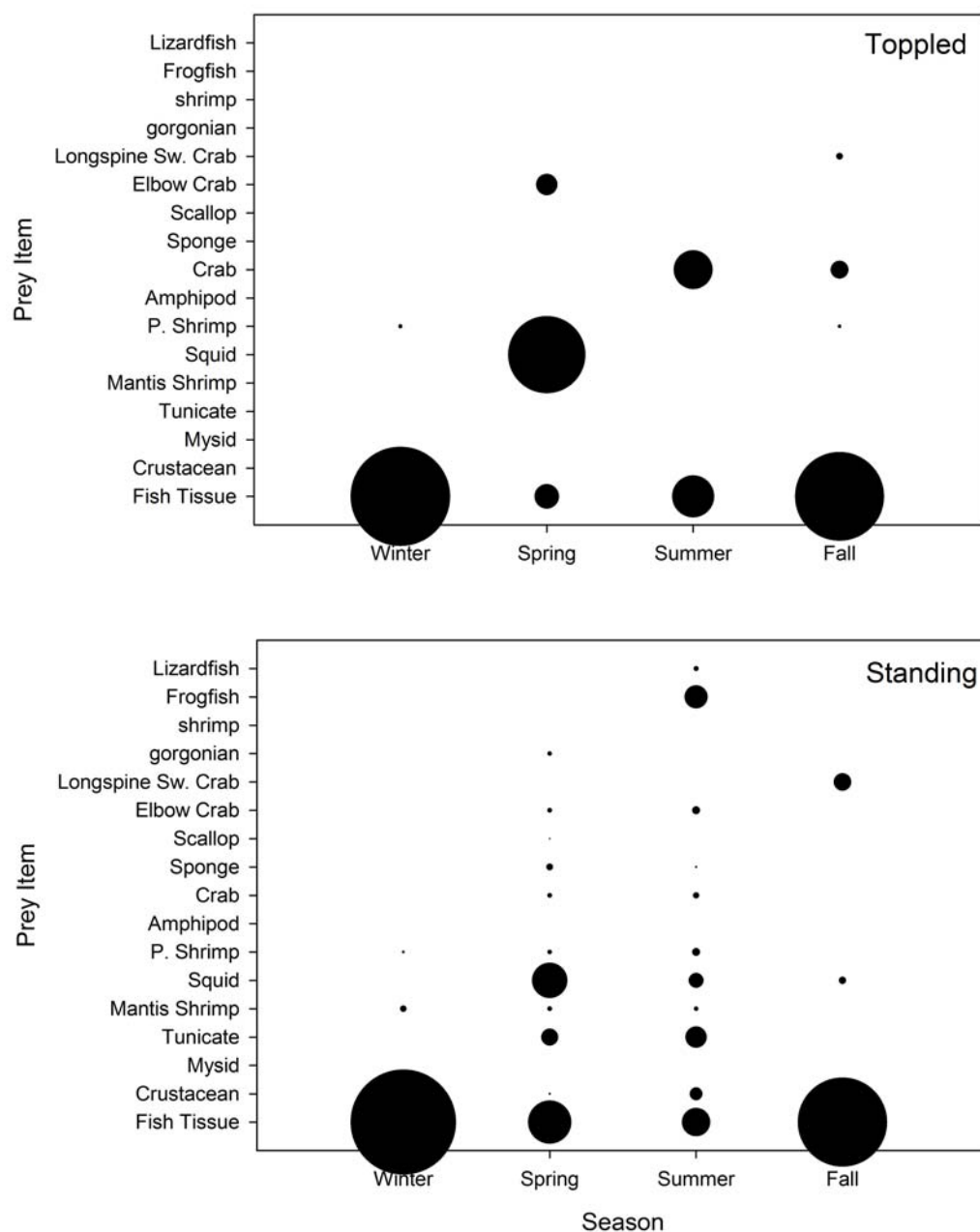


Figure 4.5: Diets of rock sea bass (*Centropristis philadelphica*) based on percentage dry weight, by season, at two different habitats including standing oil and gas platforms (standing) and toppled oil and gas platforms (toppled). Data are combined over sampling years.

(Figure 4.6). At the other distances, diets consisted of primarily crustaceans, including crabs and shrimp. The results of the IRI agree with the analysis by dry weight (Table 4.7), indicating the difference in variety in diets at the standing platforms, and the difference in proportions of fish at the toppled platforms.

Table 4.7: Percentage index of relative importance (%IRI) of rock sea bass (*Centropristis philadelphica*) diets, by distance from structure, at two different habitats including standing oil and gas platforms (standing) and toppled oil and gas platforms (toppled). Data are combined over sampling seasons and years.

Prey Item	0.25 km		0.5 km		1.0 km		1.5km	
	Standing	Toppled	Standing	Toppled	Standing	Toppled	Standing	Toppled
Fish Tissue	69.46	26.55	58.28	48.78	33.65	74.73	100.00	0
Crustacean	4.23	0	18.23	26.57	6.55	9.77	0	0
Mysid	0	30.29	0	0	0	0	0	0
Tunicate	4.10	0	0	0	3.16	0	0	0
Mantis Shrimp	2.79	0	0	0	1.46	0.84	0	0
Squid	1.46	0	0	0	19.21	11.82	0	0
P. Shrimp	10.16	0	23.49	2.95	11.11	1.96	0	56.34
Amphipod	0	0	0	0	0	0.39	0	0
Crab	4.21	43.16	0	6.92	1.00	0.48	0	0
Sponge	0.82	0	0	0	0.62	0	0	0
Scallop	0	0	0	0	0.53	0	0	0
Elbow Crab	0	0	0	11.89	20.95	0	0	0
Longspine Sw. Crab	0	0	0	2.90	0.83	0	0	43.66
Tunicate (<i>Distalpia</i> sp.)	0	0	0	0	0.94	0	0	0
Frogfish	2.12	0	0	0	0	0	0	0
Lizardfish	0.65	0	0	0	0	0	0	0

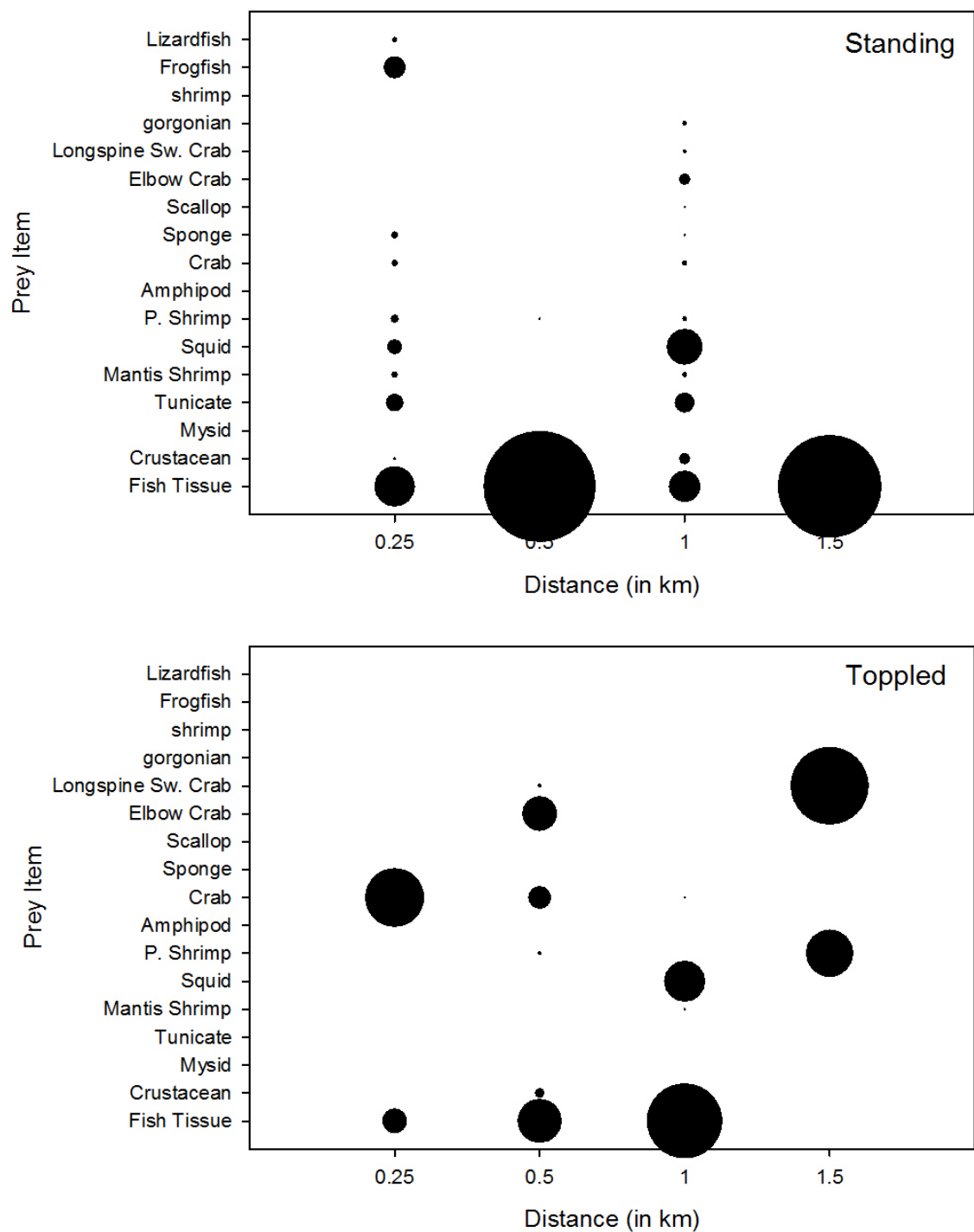


Figure 4.6: Diets of rock sea bass (*Centropristis philadelphia*) based on percentage dry weight, by distance from structure, at two different habitats including standing oil and gas platforms (standing) and toppled oil and gas platforms (toppled). Data are combined over sampling seasons and years.

Stable Isotope Analysis

No differences were observed in mean values of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, or $\delta^{34}\text{S}$ between years or among habitats, seasons, or distance from the structure ($p > 0.05$, MANCOVA). The results also indicated that mean values of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ length did not covary significantly with total length. The model was rerun as a MANOVA, however there were still no significant differences between years, between habitats, among seasons, or distance from the structure.

Though not significantly different, rock sea bass collected from the toppled platforms were more enriched in $\delta^{13}\text{C}$, though there was a greater range of $\delta^{13}\text{C}$ values from the standing platform sites (Figure 4.7). Rock sea bass were generally more enriched in $\delta^{13}\text{C}$ in the spring at the standing platforms and at in the winter at toppled platforms, though again not significantly (Figure 4.7). There no difference in mean $\delta^{13}\text{C}$ values between distances (0.25 km and 1.5km) from the structures (Figure 4.8). As compared to red snapper, rock sea bass were more enriched in $\delta^{13}\text{C}$ and the $\delta^{13}\text{C}$ range was less than that of red snapper (Figure 4.9).

There was little difference in the mean $\delta^{15}\text{N}$ values between sites and seasons (Figure 4.7). Rock sea bass were more slightly enriched in $\delta^{15}\text{N}$ in the summer months, and more depleted in the winter, though these differences were not significant (Figure 4.7). There was also no difference with distance; though rock sea bass collected 0.25 km from the toppled platforms were slightly more enriched in $\delta^{15}\text{N}$ (Figure 4.8). As compared to red snapper, rock sea bass are generally more depleted in $\delta^{15}\text{N}$, which is indicative of their smaller size and feeding at a lower trophic level (Figure 4.9).

There were no differences in the mean $\delta^{34}\text{S}$ values between sites or season (Figure 4.7). Rock sea bass were generally more enriched in $\delta^{34}\text{S}$ in the summer, and more depleted in the fall, not significantly (Figure 4.7). There were no differences in mean value of $\delta^{34}\text{S}$ with distance (Figure 4.8). Mean values of $\delta^{34}\text{S}$ were similar between rock sea bass and red snapper (Figure 4.9).

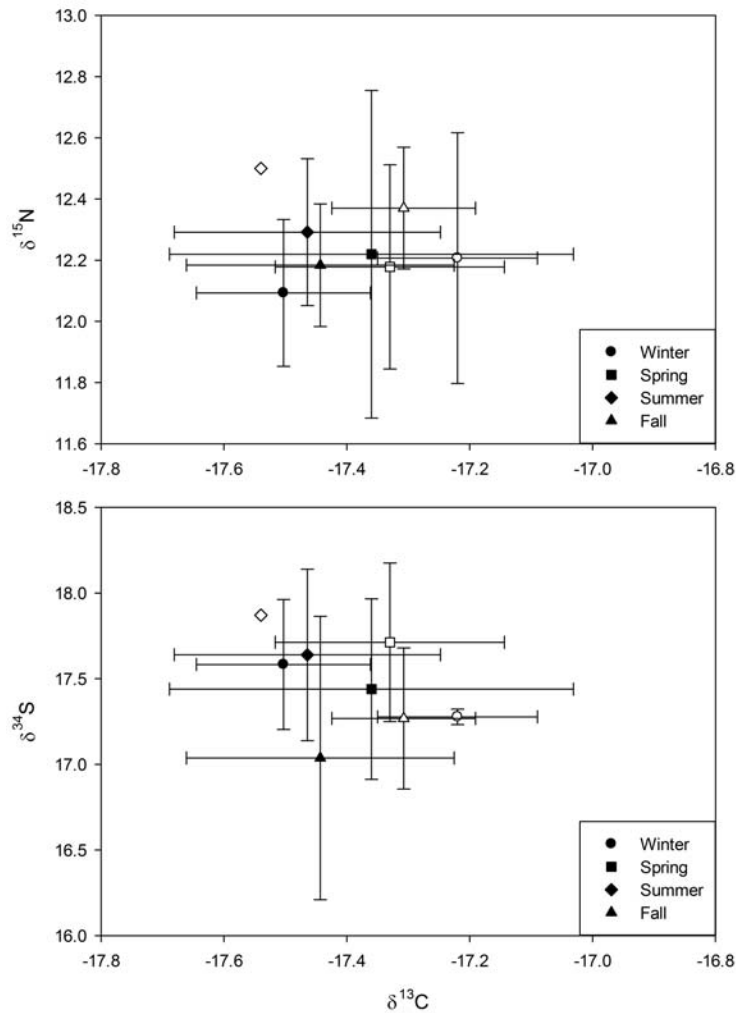


Figure 4.7: Mean stable isotope results values of rock sea bass (*Centropomus philadelphicus*) as visualized by C-N (top) and C-S (bottom) biplots for two habitats in the Gulf of Mexico, including standing (closed symbols) and toppled (open symbols) oil and gas platforms. Results are combined over years and distances, and visualized over seasons as winter (circle), spring (square), summer (diamond) and fall (triangle). Standard error bars are shown around the mean.

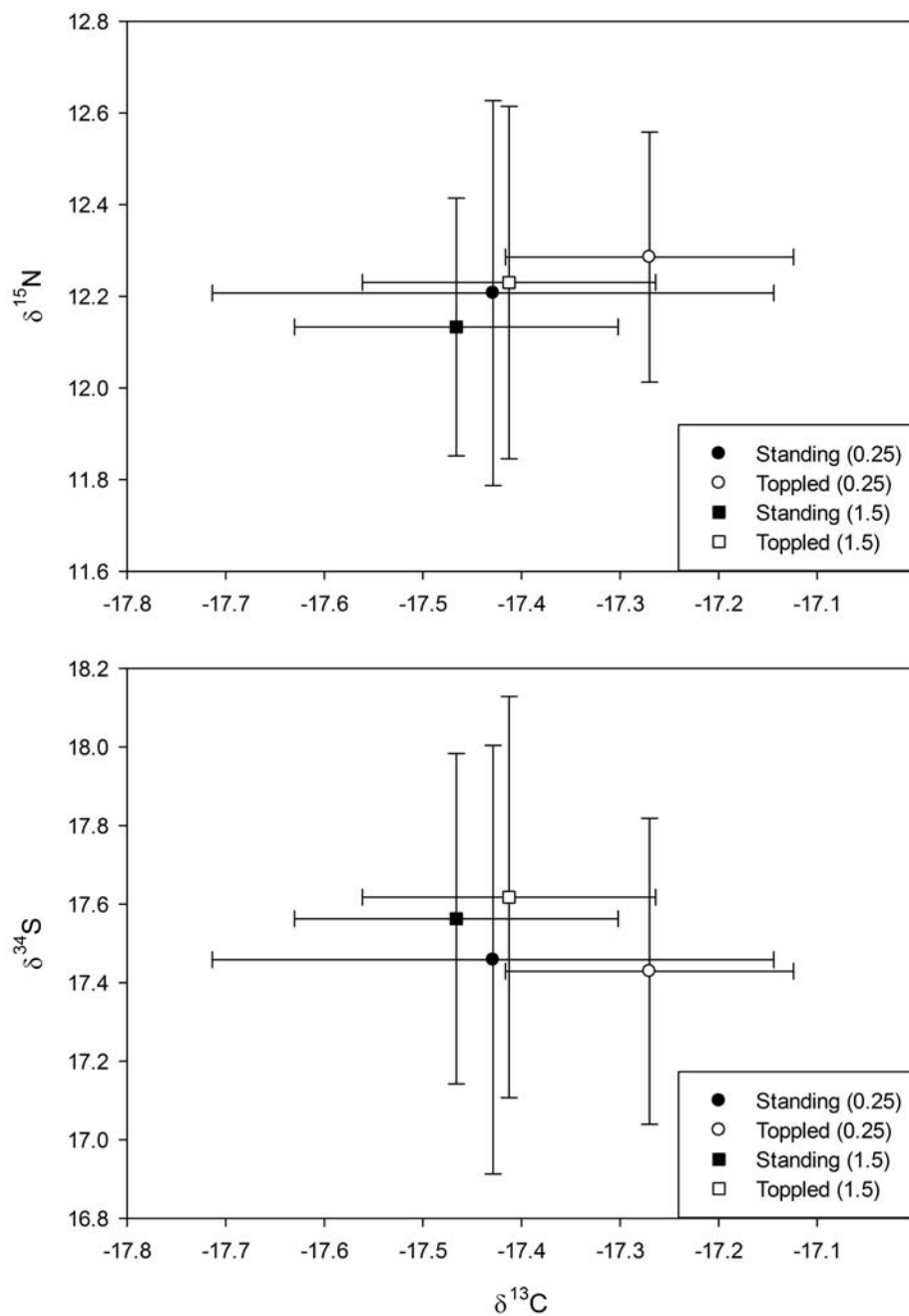


Figure 4.8: Mean stable isotope results values of rock sea bass (*Centropristis philadelphica*) as visualized by C-N (top) and C-S (bottom) biplots for two habitats in the Gulf of Mexico, including standing (closed symbols) and toppled (open symbols) oil and gas platforms. Results are combined over years and seasons to visualize differences based on distance from structure, as represented by near, 0.25km, and far, 1.5km, distances from the reef structure. Standard error bars are shown around the mean.

Community Feeding Ecology

A complimentary study to this study collected potential sources of basal carbon to the food chain (Daigle et al. 2013). Collections were completed at the two standing platforms (EI-325 and EI-346) examined in the current study during one spring and one fall sampling effort (Daigle et al. 2013). Results of the stable isotope analyses of red snapper and rock sea bass were compared to stable isotope values of potential primary producers to determine if there were differences in basal carbon sources between habitats. Primary producers included in the study as potential sources of basal carbon included phytoplankton, red algae, epiphytic algae, and green algae, and were collected at the surface, on the platform structure, and at depth (for a full description of sampling methods see Daigle et al. 2013). Results of that study indicate that phytoplankton and epiphytic algae are the likely contributors of basal carbon to the reef community (Figure 4.9). Phytoplankton had mean $\delta^{13}\text{C}$ value of -20.78‰ in the spring and -19.71‰ in the fall, while epiphytes had a mean $\delta^{13}\text{C}$ value of -18.73‰ in the spring and -15.76‰ in the fall (Table 4.8). Red algae were more depleted in $\delta^{13}\text{C}$, with a mean of -25.86‰ and -28.17‰ in the spring and fall, respectively (Table 4.8). Green algae were more depleted in fall (-19.68‰) than in the spring (-22.91‰) (Table 4.8). Based on the fractionation rate of approximately 1‰ per trophic level, and the results of the complimentary study (Daigle et al. 2013) the most likely sources of basal carbon to the reef fish community are phytoplankton and epiphytic algae (Figure 4.9).

Table 4.8: Mean values and standard deviation (sd) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of red snapper (*Lutjanus campechanus*), rock sea bass (*Centropristis philadelphia*), and four potential sources of basal carbon, including phytoplankton, red algae, epiphytes, and green algae. Samples are presented from two seasons, spring and fall. Data for fish are combined over distances.

Season	Source	$\delta^{13}\text{C}$	sd	$\delta^{15}\text{N}$	sd	Data Source
Spring	Phytoplankton	-20.78	1.31	6.33	0.96	Terrebone-Daigle 2011
	Red Algae	-25.86	3.65	2.3	2.14	
	Epiphytes	-18.73	1.36	6.34	1.75	
	Green Algae	-22.91	7.42	3.66	1.25	
	Red Snapper (Standing)	-17.61	0.40	13.38	0.99	Current Study
	Red Snapper (Toppled)	-17.99	0.48	12.70	0.89	
	Rock Sea Bass (Standing)	-17.36	0.33	12.22	0.54	
	Rock Sea Bass (Toppled)	-17.33	0.19	12.18	0.33	
Fall	Phytoplankton	-19.71	1.19	2.42	0.94	Terrebone-Daigle 2011
	Red Algae	-28.17	3.48	3.44	0.65	
	Epiphytes	-15.76	3.25	4.67	1.41	
	Green Algae	-19.68	0.11	4.15	0.08	
	Red Snapper (Standing)	-17.59	0.57	13.42	1.11	Current Study
	Red Snapper (Toppled)	-17.65	0.63	13.95	0.91	
	Rock Sea Bass (Standing)	-17.44	0.22	12.18	0.20	
	Rock Sea Bass (Toppled)	-17.31	0.12	12.37	0.20	

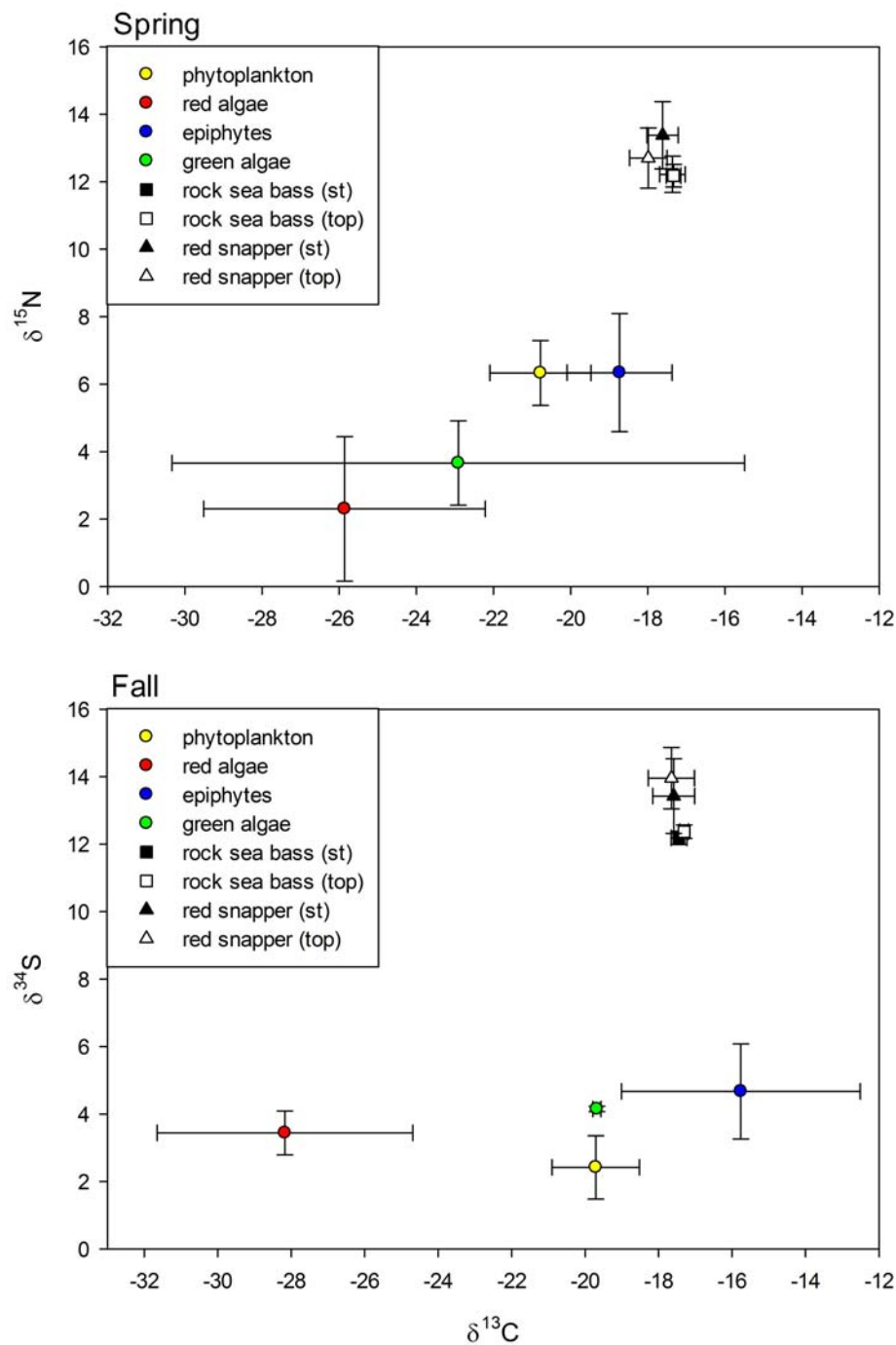


Figure 4.9: Mean stable isotope values of red snapper (*Lutjanus campechanus*; square) and rock sea bass (*Centropristis philadelphica*; triangle) as visualized by the C-N biplot at two habitats in the northern Gulf of Mexico, including standing (closed symbols) and toppled (open symbols) oil and gas platforms. Mean stable isotope values of basal resources (circle) including phytoplankton (yellow), red algae (red), epiphytes (blue) and green algae (green) are included for comparison. Isotope values of basal resources from Terrebone-Daigle, 2011. Standard error bars are shown around the mean.

Acoustic Survey

Results of the acoustic survey of the prey field surrounding the structures indicate that there are significant differences in the prey field between habitats, among seasons, and with depth and distance from the structures ($p < 0.0001$, mixed model, SAS). No data are available for the fall season due to a combination of bad weather and equipment problems during fall sampling trips. Relative prey field scattering, based on NASC, was highly variable, and differed with habitat, season, and depth (Figure 4.10). In general, NASC was higher in the spring and summer than in the winter, and was generally higher in the upper and middle water column, with two exceptions. In the summer, NASC was significantly higher at toppled platforms than standing platforms at all depth levels ($p < 0.0001$, mixed model, SAS). At standing platforms in summer NASC was higher in the lower water column than the upper and middle water columns, which had similar NASC (Figure 4.10). NASC response with distance also varied, exhibiting three distinct patterns: exponential decay, exponential growth, or relatively no pattern with distance. In general, NASC reached background levels at distances between 60 and 100 m from the structures, regardless of the pattern observed. Exponential decays were observed at the standing platforms in the upper and middle water column in summer, and the upper water column in winter, and at the toppled platforms in the upper water column in both summer and winter. Exponential increases were observed at the standing platforms in the lower water column in summer, and at the toppled platforms in the middle water column in spring, summer and winter, and the lower water column summer.

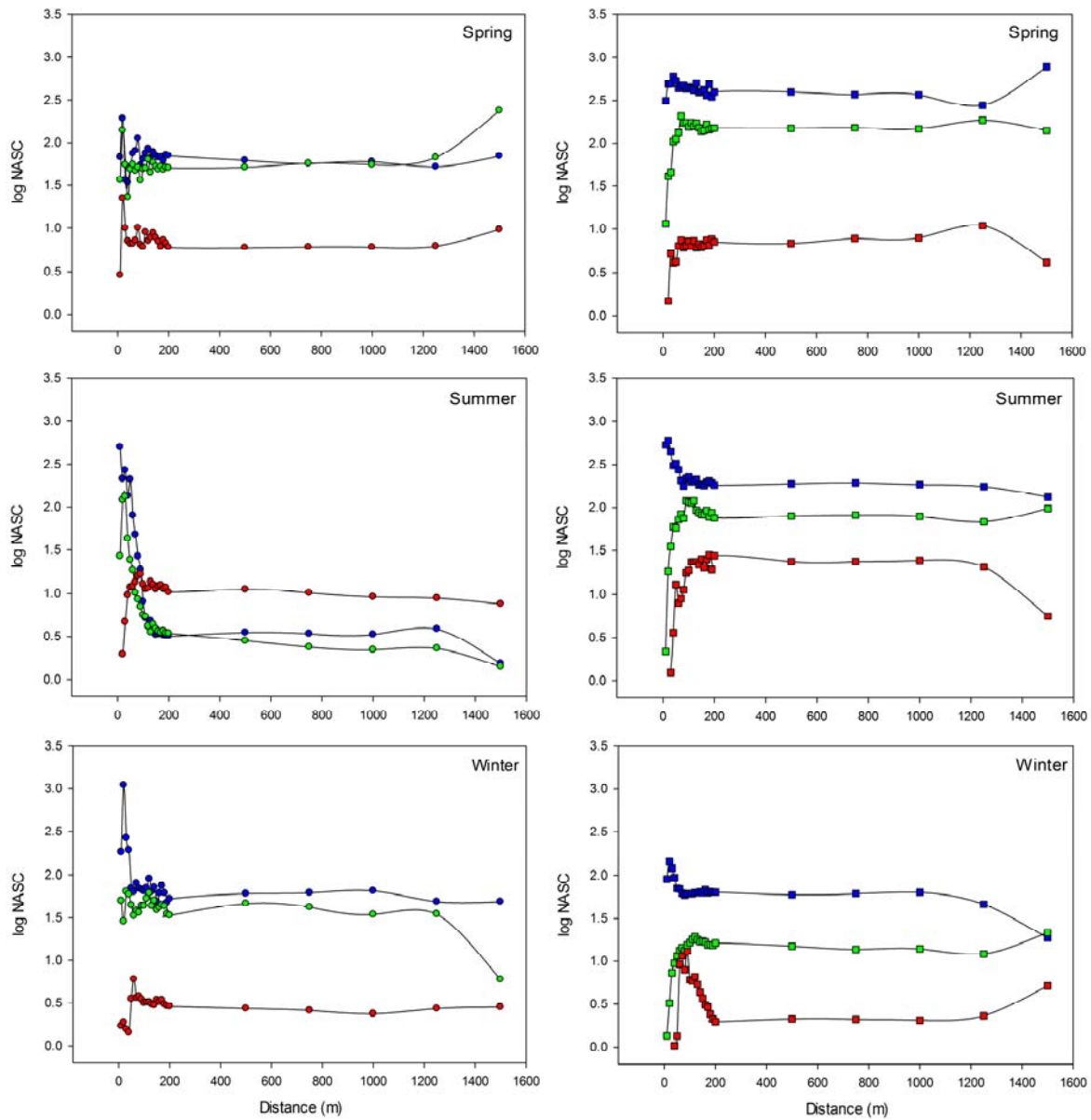


Figure 4.10: Relative biomass of potential prey field based on nautical area scattering coefficient (NASC) at two habitats in the northern GOM over a depth and distance gradient. NASC values are log transformed and plotted with distance from reef structure. Left panels represents standing platforms (circle). Right panels represent toppled platforms (square). Blue represents upper water column (0 – 30 m), green represents middle water column (30 – 60 m), and red represents lower water column (> 60 m).

Discussion

The presence of feeding halos around artificial reef structures have been well documented in regions of the eastern Gulf of Mexico and the southeast Atlantic coast of the US (Lindberg et al. 1990; Bortone et al. 1998; Lindberg et al. 2006; Shipley and Cowan), however this study represents the first attempt to quantify the presence of feeding halos around large artificial reefs in the GOM. This owes mainly to the difficulty in sampling such a large complex structure located in deep water, where visual sampling is very difficult. For this reason, many different sampling techniques were employed to assess community composition, spatial distribution and feeding ecology of reef-associated fishes. The use of traditional fishing gears such as trawls, longlines, and traps was combined with hydroacoustic surveys in an attempt to obtain a comprehensive survey of the species composition and spatial distribution around the reef sites. The use of both gut content analysis and stable isotope analysis provided a better overall assessment of the feeding ecology of reef associated fishes in the study area.

Red Snapper

Red snapper diets were consistent with previous studies, indicating that fish and crustaceans made up the majority of diets (Szedlmayer and Lee 2004; McCawley et al. 2006; McCawley and Cowan 2007; Wells et al. 2008). There were habitat specific differences in the diets of red snapper, most evident in the proportions of fish and crustaceans in the diets (also see chapter 3). Diets were also different by season, which is consistent with findings by Bradley and Bryan (1975),

who found more fish in the winter and more crustaceans in the spring and summer. This trend was also seen in the current study, and is likely influenced by a seasonal recruitment of juvenile crustaceans. The majority of the mantis shrimp and penaeid shrimp found in red snapper stomachs were small (< 30mm) and were likely juveniles. Crab megalopae also made up a significant portion of the diets by number in the summer months. This trend is confirmed by the acoustic surveys, which showed higher biomass of small planktonic scatterers in the spring and summer as compared to winter months, when such prey items were absent from the diets. In the fall and winter fish were again more abundant in the diets of red snapper, also consistent with Bradley and Bryan (1975).

Stable isotope analyses indicated significant differences between habitats and among seasons. Standing platform sites were generally more enriched in $\delta^{15}\text{N}$, than toppled platforms. This corresponds to the higher amount of fish in the diets at these sites, which exist at a higher trophic level than the crustaceans found abundantly in the diets at the toppled platforms. In the summer months, red snapper were generally more depleted in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which may be indicative of a switch in the diets during the spring months to include more shrimp, crabs and other crustaceans. Stable isotopes fully assimilate in the muscle tissue approximately 2-3 months after ingestion (Peterson and Fry 1987), which is why a shift in the diet may not be reflected in the stable isotopes until the following season. This pattern is seen again in the fall, when muscle tissue is enriched in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, reflecting the shift back to fish in the diets, especially in the fall months, when diets were almost exclusively fish. Further evidence of this pattern is

seen in the results of the basal carbon source stable isotope analyses. Fishes collected in the fall are generally more enriched in $\delta^{13}\text{C}$, which may be due in part to a larger contribution of epiphytes as a basal carbon source. This carbon source is likely to be integrated by organisms feeding directly on the reef structure, such as the crabs, shrimp, and other crustaceans found abundantly in the diets during those summer months.

The seasonal change observed in trophic niche breadth based on results of the CD analysis also reflects the seasonal shifts in prey community around these structures. The diets were far more varied in the spring and summer than in the fall and winter. This variability is reflected in the stable isotope results as an increase in CD during this time. However as previously stated, the stable isotope values in muscle tissue of fishes change on roughly the order of 2-3 months (Peterson and Fry 1987). Because of this, no differences were seen between winter and spring samples, when the seasonally abundant prey items had not been fully assimilated into the muscle tissue of red snapper. Conversely, in the fall, the presence of the seasonally abundant prey items was still evident, though the diets were far less varied, due to the long time period for assimilation into the muscle tissue.

Rock Sea Bass

The sample size for rock sea bass was much smaller than that of red snapper, and the majority of rock sea bass suffered from barotrauma and had distended stomachs. Too few samples were collected at each distance during each season to examine the habitat x distance x season interaction. Therefore, some caution should

be used in interpreting these results, as both seasonal and location differences were observed.

Little information is available on the diets of rock sea bass. Ross (1989) reported that they feed on a wide variety of organisms, including bivalves, polychaete worms, decapod crustaceans, amphipods, copepods, and fish. Rock sea bass examined in the current study fed on similar prey items, consisting of a variety of fish and large crustaceans including crabs and shrimp. The sample size for rock sea bass stomach was small, so caution should be exercised when interpreting these results. However, since so little information exists on this species, there is not much to which these results can be compared. Rock sea bass exhibited similar seasonal variability to red snapper, consuming more crustaceans in the spring and summer and more fish in the winter. Unlike red snapper, there were no significant differences in diets between habitats. Those differences that were observed were likely influenced by low sample size and therefore I cannot conclude that these were biologically significant.

Diets of rock sea bass were analyzed by distance from the structure; however, due to low sample size these data were combined over seasons. While there were differences with distance based on the results of the PERMANOVA, these results may not be biologically significant. The differences observed were detected between distances with low sample size, and are likely owing to lack of variety. The differences observed were also not seen in a gradient from the structure, i.e. the closest and farthest distances were not significantly different. Therefore, caution should be used when interpreting these results. A companion study by Terrebone-

Daigle (2011) found that there were no differences in the fish and invertebrate community with distance from the platform structures based on trawl samples. Many of the prey items found in the stomachs of rock sea bass were collected in the trawl samples analyzed by Terrebone-Daigle (2011).

Results of the stable isotope analysis indicate that rock sea bass were slightly more enriched in $\delta^{13}\text{C}$ than were red snapper, which may be contributed to the large percentage of crabs and other crustaceans in their diets. These crustaceans may be feeding directly on the structure, using a larger percentage of epiphytic algae as a basal carbon source, whereas the higher amount of fish in the diets of red snapper contain a greater percentage of phytoplankton as a basal carbon source. The fish that are found in the stomachs of rock sea bass (frogfish and lizardfish) feed close to the bottom, and may also be consuming epiphytic algae either directly or indirectly via their prey.

Acoustic Survey

Relative biomass of the potential prey base was higher in the spring and summer than in the winter samples, which corresponds to the increase in small crustaceans found in the stomachs of both reef associated fish species. This is likely evidence of an influx of larval and juvenile crustaceans to the area, which provides resources to the area. The decrease in the percentage of crustaceans in the diets in the fall and winter corresponds with the lower relative biomass observed in the winter. Patterns of relative biomass with distance varied with season, habitat, and depth, exhibiting three distinct patterns, which may help to elucidate some of the

trends observed. This is in contrast to the fish biomass observed (see Chapter 1), which consistently exhibits exponential decay with distance from the structures. The exponential growth curve observed in some of the samples may provide evidence of a feeding halo around the sites, particularly the toppled platforms, at which this pattern was observed more frequently. The lower levels of prey biomass near the structures may be indicative of higher feeding rates, especially in the lower water column, where demersal predators, such as red snapper and rock sea bass, forage. The pattern of exponential growth in prey biomass was observed at both habitats in the lower water column in the summer, when red snapper and rock sea bass consumed more small crustaceans.

If the relative prey biomass does provide evidence of a feeding halo, the zone of prey depletion would extend approximately 60 – 100 m from the structure. No differences were observed in either trap catches (Simonsen, unpublished data) or trawl tows (Terrebone-Daigle 2011) between sampling sites near (250 m) to the structure and far (1500 m) from the structure. However, it is possible that trawl and trap sets were not set close enough to the structure to observe a feeding halo, if one does exist. Sampling closer to the structure with trawls or traps was not possible due to the danger of getting equipment hung up in the reef structure. There is also no direct evidence of a decline in specific prey items from the soft bottom sediments, as sampling within that area was not feasible. Visual surveys were limited by depth, and mud samples collected with a ponar grab (Terrebone-Daigle 2011) could not be safely conducted closer than 250 m from the structure. Therefore, while the hydroacoustic results may provide some empirical evidence of

a seasonal halo effect, some caution should be exercised when interpreting these results.

Community Feeding Ecology

The data collected during this study provide contradictory evidence for the presence of feeding halos. In general, very few red snapper (8% of total catch at standing and toppled platforms combined) were found at distances greater than 0.25km away from the structures. The assumption was that if red snapper were making foraging migrations away from the platform structures, they would have been vulnerable to our gear. Wells et al. (2008b) determined that the same chevron fish trap used in this study had high catchability compared to other gear types analyzed. However, there is also a chance that they were utilizing regions away from the structure for foraging and were not captured by sampling gear. The area sampled in this study was much larger than that sampled by Wells et al. (2008b), and so catchabilities are not directly comparable. Nevertheless, low catch totals at distance from the structure, and high catch totals directly adjacent to the structure may indicate less range of foraging, at least for these sites. McDonough (2009) showed a maximum detectable range of acoustically tagged red snapper to be on the order of 350m from the platform structure at which it was tagged. While there is some evidence that tagged fish moved beyond the range of detection and subsequently returned to the same site, the home range reported by McDonough (2009) is similar to that shown here, with most fish staying within 500m of the site. Additionally, hydroacoustic data indicates the “area of influence” in the water column around these sites to be out to approximately 100m from the site, before

dropping off to background levels (Chapter 1). The most likely cause for this is high risk of predation at these sites, as large pelagic predators such as barracuda (*Sphyraena barracuda*), amberjack (*Seriola dumerili*), king mackerel (*Scomberomorus cavalla*) and many species of sharks were frequently observed in high numbers. Foraging migrations are an energy and mortality trade-off (Biesinger et al. 2011), and foraging migrations are only energetically efficient if the caloric intake from doing so is high enough to offset the energetic demands of swimming and searching, and the risk of predation is sufficiently low. Based on visual and acoustic observations of these sites, that may not be the case, particularly at standing platforms where upper water column structure aggregates large pelagic predators.

The diet and stable isotope results provide little evidence that feeding halos exist. Though sample sizes were low, there were no differences in diets of rock sea bass with distance. There were also no differences in mean values of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, or $\delta^{34}\text{S}$ with distance. However, sampling was limited by the ability to safely set gear near the structures. It is possible that if samples were collected at intervals between 0 and 250 m from the structures, that differences would have been observed. Regardless, results of the stable isotope analysis of both fish species examined here and the basal carbon sources analyzed by Daigle et al. (2013) indicate that basal carbon is consistently sourced from phytoplankton and, to a lesser degree, epiphytic algae. The lack of differences in both red snapper and rock sea bass stable isotope signatures with distance, along with the results reported by Daigle et al. (2013) indicate that sources basal carbon do not change with distance from the structures.

The differences observed in the trophic ecology of both red snapper and rock sea bass appear to be seasonally influenced, or habitat specific. Potential explanations for these observations are detailed below.

This study has shown evidence of both temporal and site-specific trends in diets of both red snapper and rock sea bass. For both species, an increase in the amount of crustacean prey was observed in the spring and summer months, at both habitats. This pattern was influenced by an abundance of crabs, mantis shrimp, and penaeid shrimp, all of which were observed to be in larval or juvenile stages, and coincided with an increase in the relative biomass of potential prey observed in the acoustic surveys. The acoustic surveys did provide some evidence of a halo effect, particularly in the observed increase in relative biomass at distances of 60 – 100 m from the structures during both spring and summer. Furthermore, this pattern was observed more regularly at toppled platforms, which had higher proportion of crustaceans in the diets of red snapper than those collected at standing platforms. A higher percentage of diets at the standing platforms consisted of fish, particularly antennae codlet. When found, this prey item was found in high numbers in individual stomachs. Video observations of the sites from ROV footage showed large schools of antennae codlet that were attracted to the lights of the ROV. The most likely explanation is that teleost prey is attracted to the lights of the platform, which have been shown to have a large effect on the surrounding fish assemblage (Keenan et al. 2007). Squid were also found in higher numbers at the standing platform sites, and there is substantial evidence of squid being attracted to light fields as well. The presence of this schooling fish species and, to a lesser degree, squid may provide

suitable prey for red snapper, diminishing the need for crustacean and zooplankton prey, resulting in less intense zones of prey depletion and less evidence of halos in the acoustic returns.

In conclusion, the trophic ecology of the large artificial reefs examined in this study is influenced more by seasonal trends and site-specific prey availability, which does not change with distance from the structure. While some ancillary evidence of feeding halos may exist in the relative biomass of the zooplankton prey base, reef-associated fish prey appears to be consistently sourced from the surrounding soft bottom sediments and water column, and basal carbon sources were consistent throughout the study area. Further sampling needs to be conducted of the plankton and epibenthic communities at intervals within 100 m of large artificial reefs structures in order to conclusively quantify the presence of feeding halos.

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GENERAL SUMMARY AND CONCLUSIONS

The two objectives of this study were to examine the high-resolution spatial and temporal distribution of reef-associated fish biomass around standing and toppled oil and gas platforms, and to examine the habitat effects on trophic dynamics of common reef-associated fish species, such as red snapper (*Lutjanus campechanus*). The use of a mobile hydroacoustic approach to assessing biomass distribution allowed for fine scale examination of biomass distribution over space and time. However, this approach is limiting in that no direct information on species composition is available. Trophic dynamics were assessed with a combination of gut content and stable isotope analyses to obtain a thorough understanding of how habitat affects not only the prey, but the sources of basal resources. Trophic dynamics were assessed over three habitats, including natural shelf edge banks, where very little information exists on red snapper feeding ecology in general. The same approach was used to assess whether a zone of prey depletion, a “feeding halo”, had developed around large artificial reefs. This project also sought to address the lack of information that exists on reef fish ecology at the natural shelf edge banks and toppled platforms in the Gulf of Mexico.

Chapter 1 examined the spatial distribution of nekton around standing and toppled platforms using a multifrequency hydroacoustic approach, which allowed for the separation of fish and zooplankton from the echograms in order to more accurately assess distribution of fish. The multifrequency approach also provided the means to classify scatterers into broad groups, based on their frequency response. This combination of techniques not only provided high-

resolution information on nekton distribution, but also provided a means to examine how habitat affected specific classes of organisms. The strength of this approach was that it provided a means to determine not only that mean volume backscatter (MVBS) was higher in the upper water column at standing platforms, but identify the likely contributors to this difference. Analysis of the four specific classes of organisms developed revealed that large pelagic predators and schooling planktivores were found to have higher MVBS at the standing platforms, likely contributed to the higher over MVBS at the standing platforms. There were limitations to this technique, primarily in that effective groundtruthing of the classification was not possible. Future studies incorporating a multifrequency approach should include techniques to groundtruth the acoustic data, which will provide a more robust overall analysis.

In Chapter 2, the mobile hydroacoustic approach was used to examine changes in biomass distribution on a diel cycle, using the approach to acoustic data analysis developed in Chapter 1. Here, fish scatterers were examined over a 48-hour period at both habitats to determine if diel patterns were influenced by habitat. Analyses revealed diel periodicity, characterized by higher MVBS in the upper and middle water column at night, and higher MVBS in the lower water column during the day. This diel distribution was also affected by habitat and distance from the structure. While diel periodicity remained relatively consistent at toppled platforms, the diel pattern broke down in close range to the standing platforms. This is likely an effect of light being emitted from the operational standing platforms, causing disruption of normal diel movements. Additionally, the

classes of scatterers identified in Chapter 1 as having higher MVBS near standing platforms are known to be associated with the oil and gas platforms for increased foraging opportunities, due in part to the aggregation of key prey items in the lights.

Chapter 3 examined the trophic dynamics of red snapper at three distinct habitats in the northern Gulf of Mexico. Despite the high recreational value of the species, high catch totals off the Louisiana coast, and extensive work conducted on the species in the eastern Gulf and off the Texas coast, there was little information on red snapper off the coast of Louisiana, and even less information on fish collected from natural habitats. One theory on artificial reefs is that they provide unique prey resources to reef-associated fishes such as red snapper. This chapter concluded that the opposite was true, as there were specific prey items absent from diets of red snapper at each artificial reef habitat that were found at the natural shelf edge back habitat. However, the results also emphasized the opportunistic nature of red snapper, revealing that, regardless of habitat, basal resources were consistently sources from the surrounding water column and soft bottom sediments. The natural banks examined in this study were among the closest to the Mississippi River, and therefore less complex than banks further east, characterized by sand and mud and lower diversity of coral. Future comparisons of trophic ecology on these habitat types should aim to include the higher relief, more complex shelf edge banks farther west.

Chapter 4 further examined the trophic ecology of reef-associated fishes, using two common species, red snapper and rock sea bass (*Centropristis philadelphica*) to specifically determine if a feeding halo existed around standing

and toppled oil and gas platforms. As with Chapter 3, there were habitat specific differences in the diets, but analysis of stable isotope ratios indicated that basal resources were consistently sourced from the surrounding water column and soft bottom sediments. Furthermore, there were no differences in the diets or stable isotope ratios with distance from the reef structures in either species. The limitation of this study was that data could not be safely collected closer than 250 m from the reef structures. Results of Chapter 1 indicated that the area of influence of the platform was approximately 100 m from the structures. Therefore, it is possible that a halo does exist, but was not detected with this methodology. Analysis of acoustic data processed to include zooplankton and other potential prey in Chapter 1 was used to examine distribution of the potential prey base, though only provided ancillary evidence of a feeding halo. Areas of lower prey biomass were observed within 100 m of the platform structures, however there is no evidence that this is directly related to predation.

Results of this study provide insight into how these structures function as reef-associated fish habitat. In general, the standing platforms support higher fish biomass, characterized by schooling planktivores and large pelagic predators, which are likely using the standing platforms for increased foraging opportunities. Diets of red snapper at standing platforms contained a large number of antenna codlet (*Bregmaceros atlanticus*), which are known to be phototactic. The most influential aspect of the standing platforms may therefore be the presence of the light field emitted by the operational platforms. The evidence suggests that lights may be acting to aggregate prey species, and disrupt normal patterns of diel migration.

Because both of the standing platforms were operational, and emitting light, it is not possible to determine if the differences observed are due to the presence of structure in the upper water column, due to the light field, or due to the combination of the two. An interesting comparison would be to examine a standing platform that is no longer in operation, and therefore not emitting a strong light field.

Whatever the cause, this study has shown different patterns of use between the two habitats, which is likely species specific. MVBS in the lower water column was similar between habitats, indicating that the distribution of demersal species is likely not as influenced by the type of structure. Conversely, there were differences in MVBS and distribution of specific classes the upper water column between habitats, including higher biomass of large pelagic predators. If this is the case, then the presence of large pelagic predators is likely exerting a top-down control on the standing platform system. Overall, the presence of large artificial reefs such as those examined in this study likely affect different species in different ways. The effectiveness of decommissioned platforms as artificial reefs is therefore subject to the species of interest, as they are likely to benefit demersal species more than pelagic predators or schooling planktivores. Future studies on the efficacy of large artificial reefs should focus on the specific aspects of the habitat that benefit the various groups of reef-associated fishes that inhabit these large structures.

APPENDIX A: CHAPTER 3 SUPPLEMENTARY DATA

Presence/absence of all prey items collected during June and July of 2009 and 2010 in red snapper (*Lutjanus campechanus*) stomachs at three habitats in the northern Gulf of Mexico, including standing oil and gas platforms (standing), toppled oil and gas platforms (toppled) and natural shelf edge banks (bank). Prey items were identified to lowest taxonomic level possible. Results are shown for 2009 and 2010 separately. Presence indicated by “x”. Absence indicated by blank.

Prey Category	Prey Item	2009			2010		
		Bank	Toppled	Standing	Bank	Toppled	Standing
Fish	Unidentified Tissue	x	x	x	x	x	x
	Unidentified Fish	x	x	x	x	x	x
	Tetradontiformes	x					
	<i>Synodus</i> sp.	x		x			
	<i>Bregmaceros atlanticus</i>	x		x	x		x
	<i>Trichiurus lepturus</i>	x					
	<i>Micropogonias undulatus</i>		x				
	<i>Trachurus lathami</i>	x			x		
	<i>Urophycis</i> sp.					x	
	<i>Porichthys plectodon</i>		x				
Crustaceans	Unidentified Crustacean	x	x	x	x		x
	Penaeidae	x		x			
	<i>Squilla</i> sp.	x	x	x	x	x	x
	Unidentified Brachyura	x	x		x		

(continued)

		1	2	3	4	5	6	7
Benthic Zooplankton	<i>Pseudomedeus agassizii</i>						x	
	Leucosiidae	x					x	
	<i>Bathynectes longispina</i>	x	x					
	Portunidae	x	x		x			
	Galatheidae	x						
	Hepatidae	x					x	
	Mysidae	x						
Pelagic Zooplankton	Isopoda	x	x				x	
	Hyperid Amphipod	x	x		x			
	Amphipoda	x	x		x		x	x
	Cavalina (pteropod)			x	x		x	x
	Crab Megalop			x	x		x	x
Mollusc	Squid	x	x		x		x	x
	Unidentified Mollusc	x						
	Unidentified Bivalve	x						
Cnidarian	Anemone	x						
	Hydroid						x	x
Porifera	Sponge	x	x		x			

(continued)

Chordata	Colonial Tunicate (<i>Distaplia</i> sp.)		x	x	x	x
Worms	Unidentified Worm		x	x		
	Polychaete	x		x	x	
Other	Detritus	x				
	Hard Coral Fragments	x				
	Egg Mass		x			

Frequency of occurrence (FO) of all prey items collected during June and July of 2009 and 2010 in red snapper (*Lutjanus campechanus*) stomachs at three habitats in the northern Gulf of Mexico, including standing oil and gas platforms (standing), toppled oil and gas platforms (toppled) and natural shelf edge banks (bank). Prey items were identified to lowest taxonomic level possible. Results are shown for 2009 and 2010 separately. Total FO for all habitats and all years is also shown.

Prey Category	Prey Item	2009			2010			Total
		Bank	Toppled	Standing	Bank	Toppled	Standing	
Unidentified	Unidentified Tissue	0.157	0.122	0.066	0.333	0.292	0.333	0.156
Fish	Unidentified Fish	0.236	0.102	0.226	0.311	0.125	0.292	0.215
	Tetradontiformes	0.004	0	0	0	0	0	0.002
	<i>Synodus</i> sp.	0.011	0	0.015	0	0	0	0.008
	<i>Bregmaceros atlanticus</i>	0.094	0	0.131	0.044	0	0.042	0.077
	<i>Trichiurus lepturus</i>	0.004	0	0	0	0	0	0.002
	<i>Micropogonias undulatus</i>	0	0.010	0	0	0	0	0.002
	<i>Trachurus lathami</i>	0.004	0	0	0.022	0	0	0.003
	<i>Urophycis</i> sp.	0	0	0	0	0.042	0	0.002
	<i>Porichthys plectodon</i>	0	0.010	0	0	0	0	0.002
Crustaceans	Unidentified Crustacean	0.139	0.194	0.131	0.089	0	0.042	0.133
	Penaeidae	0.067	0.000	0.051	0.089	0.042	0.042	0.052
	<i>Squilla</i> sp.	0.004	0.020	0.015	0.156	0.417	0.083	0.040
	Unidentified Brachyura	0.064	0.020	0	0.044	0	0	0.035

(continued)

	<i>Pseudomedaeus agassizii</i>	0	0	0	0.022	0	0	0.002
	Leucosiidae	0.004	0	0	0.044	0	0	0.005
	<i>Bathynectes longispina</i>	0.004	0.041	0	0	0	0	0.008
	Portunidae	0.004	0.010	0.007	0	0	0	0.005
	Galatheidae	0.015	0	0	0	0	0	0.007
	Hepatidae	0.007	0	0	0.022	0	0	0.005
Benthic Zooplankton	Mysid	0.007	0	0	0	0	0	0.003
	Isopod	0.004	0.010	0	0.156	0	0	0.015
	Hyperid Amphiod	0.007	0.102	0.022	0	0	0	0.025
	Amphipod	0.011	0.020	0.051	0.178	0.167	0	0.040
Pelagic Zooplankton	<i>Cavalina</i> sp. (pteropod)	0	0.010	0.007	0.156	0.208	0.042	0.025
	Crab Megalop	0	0.082	0.007	0.111	0.042	0	0.025
Mollusc	Squid	0.030	0.051	0.073	0.067	0.042	0.167	0.052
	Unidentified Mollusc	0.022	0	0	0	0	0	0.010
	Unidentified Bivalve	0.011	0	0	0	0	0	0.005
Cnidarian	Anemone	0.011	0	0	0	0	0	0.005
	Hydroid	0	0	0	0.044	0.042	0	0.005
Porifera	Sponge	0.004	0.010	0.022	0	0	0	0.008
Chordata	Colonial Tunicate (<i>Distaplia</i> sp.)	0	0	0.015	0.200	0.583	0.083	0.045
Worm	Worm	0	0	0.007	0.022	0	0	0.003
	Polychaete	0	0.010	0	0.156	0.208	0	0.022

(continued)

Other	Detritus	0.011	0	0	0	0	0	0.005
	Hard Coral Fragments	0.011	0	0	0	0	0	0.005
	Egg Mass	0	0	0.007	0	0	0	0.002

Mean values of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ for red snapper (*Lutjanus campechanus*) collected over three habitat types in the Gulf of Mexico, including standing oil and gas platforms (standing), toppled oil and gas platforms (toppled) and natural shelf-edge bank (bank) habitat, per year. Total number of samples run (n) and standard deviations (SD) are also shown.

Habitat	Year	n	Mean $\delta^{15}\text{N}$	SD	Mean $\delta^{13}\text{C}$	SD	Mean $\delta^{34}\text{S}$	SD
Standing	2009	48	12.30	0.90	-18.14	0.46	18.05	0.72
	2010	16	13.59	1.26	-17.47	0.70	17.60	1.01
Toppled	2009	23	12.26	0.67	-18.18	0.53	16.99	0.38
	2010	16	12.78	1.36	-18.05	0.70	17.65	0.75
Bank	2009	178	12.45	0.85	-17.48	2.38	18.19	3.03
	2010	36	12.45	0.69	-17.78	0.36	18.15	0.48

Mean values and standard deviation (sd) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for four potential sources of basal carbon, including phytoplankton, red algae, epiphytes, and green algae collected at standing platforms in the northern Gulf of Mexico. Samples are presented from collections in both spring and fall 2010.

Season	Source	$\delta^{13}\text{C}$	sd	$\delta^{15}\text{N}$	sd	Data Source
Spring	Phytoplankton	-20.78	1.31	6.33	0.96	Terrebone-Daigle 2011
	Red Algae	-25.86	3.65	2.3	2.14	
	Epiphytes	-18.73	1.36	6.34	1.75	
	Green Algae	-22.91	7.42	3.66	1.25	
Fall	Phytoplankton	-19.71	1.19	2.42	0.94	Terrebone-Daigle 2011
	Red Algae	-28.17	3.48	3.44	0.65	
	Epiphytes	-15.76	3.25	4.67	1.41	
	Green Algae	-19.68	0.11	4.15	0.08	

APPENDIX B: CHAPTER 4 SUPPLEMENTARY DATA

Presence/absence of all prey items collected during all seasons in 2009 and 2010 in red snapper (*Lutjanus campechanus*) stomachs at two habitats in the northern Gulf of Mexico, including standing oil and gas platforms (standing) and toppled oil and gas platforms (toppled). Prey items were identified to lowest taxonomic level possible. Results are shown each habitat and season separately. Presence indicated by “x”. Absence indicated by blank.

Prey		Standing				Toppled			
Category	Prey Item	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
Fish	Unidentified Tissue	x	x	x	x	x	x	x	
	Unidentified Fish	x	x	x	x	x	x	x	x
	<i>Prionotus stearnsi</i>				x				
	Tetradontiformes				x				
	Triglidae	x			x				
	Balistidae						x		
	<i>Synodus</i> sp.	x		x			x		
	<i>Bregmaceros atlanticus</i>	x	x	x					
	<i>Micropogonias undulatus</i>					x		x	
	Phycidae							x	
	<i>Selene</i> sp.			x					
	<i>Porichthys</i> sp.							x	
	Unidentified Crustacean	x	x	x	x	x	x	x	x
	Penaeid Shrimp	x	x	x	x	x	x	x	
	<i>Squilla</i> sp.	x	x	x	x	x	x	x	
Crustacean	Unidentified Brachyura	x	x	x				x	

(continued)

		Benthic							
		Zooplankton							
		Pelagic							
		Zooplankton							
		Mollusc							
		Cnidarian							
		Profera							
		Chordate							
		Worm							
		Other							
	<i>Bathynectes</i>								x
	<i>longispina</i>								
	Portunidae			x					x
	<i>Leiolambrus</i>					x			
	<i>nitidus</i>								
Benthic									
Zooplankton	Amphipoda		x	x			x		x
	Hyperid Amphiod		1	x			x		x
	Isopoda								x
Pelagic									
Zooplankton	Crab Megalop	x		x			x		x
	Cavalina (pteropod)		x	x	x		x		x
Mollusc	Squid	x	x	x	x	x	x	x	x
	Unidentified		x						
	Gastropod								
	Unidentified								
	Mollusc						x		
Cnidarian	Hydroid		x				x		x
Profera	Sponge	x		x					x
	Colonial Tunicate								
Chordate	(<i>Distaplia</i> sp.)			x					x
Worm	Worm			x					
	Polychaete		x	x					x
Other	Egg			x					
	Detritus	x				x			

Frequency of occurrence (FO) of all prey items collected all seasons in 2009 and 2010 in red snapper (*Lutjanus campechanus*) stomachs at two habitats in the northern Gulf of Mexico, including standing oil and gas platforms (standing) and toppled oil and gas platforms (toppled). Prey items were identified to lowest taxonomic level possible. Results are shown each habitat and season separately.

Prey Category	Prey Item	Standing				Toppled			
		Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
Fish	Unidentified Tissue	0.16	0.14	0.12	0.27	0.17	0.22	0.16	0
	Unidentified Fish	0.22	0.20	0.24	0.18	0.09	0.11	0.11	0.57
	<i>Prionotus stearnsi</i>	0	0	0	0.01	0	0	0	0
	Tetradontiformes	0	0	0	0.01	0	0	0	0
	Triglidae	0.01	0	0	0.01	0	0	0	0
	Balistidae	0	0	0	0	0	0.01	0	0
	<i>Synodus</i> sp.	0.02	0	0.02	0	0	0.01	0	0
	<i>Bregmaceros atlanticus</i>	0.02	0.06	0.11	0	0	0	0	0
	<i>Micropogonias undulatus</i>	0	0	0	0	0.01	0	0.01	0
	Phycidae	0	0	0	0	0	0	0.01	0
	<i>Selene</i> sp.	0	0	0.01	0	0	0	0	0
Crustacean	<i>Porichthys</i> sp.	0	0	0	0	0	0	0.01	0
	Unidentified Crustacean	0.05	0.17	0.12	0.10	0.10	0.22	0.16	0.29
	Penaeid Shrimp	0.04	0.04	0.04	0.01	0.01	0.10	0.01	0
	<i>Squilla</i> sp.	0.02	0.02	0.05	0.01	0.02	0.05	0.10	0
	Unidentified Brachyura	0.01	0.01	0.01	0	0	0	0.02	0
	<i>Bathynectes longispina</i>	0	0	0	0	0	0	0.03	0

(continued)									
	Portunidae	0	0	0.01	0	0	0	0.01	0
	<i>Leiolambrus</i>								
	<i>nitidus</i>	0	0	0	0	0.01	0	0	0
Benthic									
Zooplankton	Amphipoda	0	0.01	0.04	0	0	0.05	0.05	0
	Hyperid Amphiod	0	0.01	0.02	0	0	0.07	0.08	0
	Isopoda	0	0	0	0	0	0	0.01	0
Pelagic									
Zooplankton	Crab Megalop	0.01	0	0.01	0	0	0.02	0.07	0
	Cavalina								
	(pteropod)	0	0.01	0.02	0.01	0	0.03	0.05	0
Mollusc	Squid	0.02	0.09	0.08	0.02	0.02	0.06	0.05	0.14
	Unidentified								
	Gastropod	0	0.02	0	0	0	0	0	0
	Unidentified								
	Mollusc	0	0	0	0	0	0.01	0	0
Cnidarian	Hydroid	0	0.01	0	0	0	0.01	0.01	0
Profera	Sponge	0.01	0	0.02	0	0	0	0.01	0
	Colonial Tunicate								
Chordate	(<i>Distaplia</i> sp.)	0	0	0.02	0	0	0	0.11	0
Worm	Worm	0	0	0.01	0	0	0	0	0
	Polychaete	0	0.03	0.01	0	0	0	0.05	0
Other	Egg	0	0	0.01	0	0	0	0	0
	Detritus	0.01	0	0	0	0.01	0	0	0

Mean values of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ for red snapper (*Lutjanus campechanus*) collected over two habitat types in the Gulf of Mexico, including standing oil and gas platforms (standing) and toppled oil and gas platforms (toppled) habitat, by season, combined over years. Total number of samples run (n) and standard deviations (sd) are also shown.

Season	Habitat	N	$\delta^{15}\text{N}$	sd	$\delta^{13}\text{C}$	sd	$\delta^{34}\text{S}$	sd
Winter	Standing	38	13.19	0.96	-17.51	0.35	17.69	0.82
	Toppled	22	12.25	0.97	-17.99	0.60	17.71	0.53
Spring	Standing	42	13.38	0.99	-17.61	0.40	17.65	0.86
	Toppled	49	12.70	0.89	-17.99	0.48	17.80	0.50
Summer	Standing	88	12.76	1.15	-17.93	0.58	17.79	0.92
	Toppled	57	12.28	1.05	-18.22	0.53	17.63	0.90
Fall	Standing	50	13.42	1.11	-17.59	0.57	17.59	0.95
	Toppled	7	13.95	0.91	-17.65	0.63	18.05	0.43

Presence/absence of all prey items collected during all seasons in 2009 and 2010 in rock sea bass (*Centropristis philadelphica*) stomachs at two habitats in the northern Gulf of Mexico, including standing oil and gas platforms (standing) and toppled oil and gas platforms (toppled). Prey items were identified to lowest taxonomic level possible. Results are shown each habitat and season separately. Presence indicated by “x”. Absence indicated by blank.

Prey Category	Prey Item	Standing				Toppled			
		Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
Unidentified	Unidentified	x	x		x	x	x	x	x
Fish	Unidentified Fish Tissue	x	x	x	x		x	x	x
	<i>Antennarius</i> sp.			x					
	<i>Synodus</i> sp.			X					
Crustacean	Unidentified Crustacean		x	x			x		x
	<i>Squilla</i> sp.		x	x	x		x		
	Penaeid Shrimp	x	x	x	x	x	x		x
	Unidentified Brachyura		x	x				x	x
	Parthenopidae		x	x			x		
	<i>Portunus spinicarpus</i>				x				x
Benthic Zooplankton	Mysid					x			
	Amphipod						x		
Mollusc	Squid		x	x	x		x		
	Scallop		x						
Cnidarian	Hydroid		x	x					

(continued)

Porifera	Sponge	x	x
	Colonial		
	Tunicate	x	
Chordate	<i>(Distalpia sp.)</i>		

Frequency of occurrence (FO) of all prey items collected during all seasons in 2009 and 2010 in rock sea bass (*Centropristis philadelphica*) stomachs at two habitats in the northern Gulf of Mexico, including standing oil and gas platforms (standing) and toppled oil and gas platforms (toppled). Prey items were identified to lowest taxonomic level possible. Results are shown each habitat and season separately.

Prey		Standing				Toppled			
Category	Prey Item	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
Unidentified	Unidentified	0.50	0.33	0	0.62	0.75	0.17	0.67	0.25
Fish	Unidentified								
	Fish Tissue	0.50	0.33	0.82	0.23	0	0.50	0.33	0.40
	<i>Antennarius</i>								
	sp.	0	0	0.09	0	0	0	0	0
Crustacean	<i>Synodus</i> sp.	0	0	0.09	0	0	0	0	0
	Unidentified								
	Crustacean	0	0.42	0.18	0	0	0.17	0	0.30
	<i>Squilla</i> sp.	0	0.08	0.09	0.08	0	0.17	0	0
	Penaeid								
	Shrimp	0.13	0.50	0.09	0.08	0.25	0.17	0	0.05
	Unidentified								
	Brachyura	0	0.08	0.27	0	0	0	0.33	0.10
	Parthenopidae	0	0.17	0.09	0	0	0.17	0	0
Benthic	<i>Portunus</i>								
	<i>spinicarpus</i>	0	0	0	0.08	0	0	0	0.10
Zooplankton	Mysid	0	0	0	0	0.25	0	0	0
	Amphipod	0	0	0	0	0	0.17	0	0
Mollusc	Squid	0	0.17	0.09	0.08	0	0.50	0	0

(continued)

	Scallop	0	0.08	0	0	0	0	0	0
Cnidarian	Hydroid	0	0.17	0.09	0	0	0	0	0
Porifera	Sponge	0	0.08	0.09	0	0	0	0	0
	Colonial								
	Tunicate								
Chordate	(<i>Distalpia</i> sp.)	0	0.08	0	0	0	0	0	0

Mean values of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ for rock sea bass (*Centropristis philadelphica*) collected over two habitat types in the Gulf of Mexico, including standing oil and gas platforms (standing) and toppled oil and gas platforms (toppled) habitat, by season, combined over years. Total number of samples run (n) and standard deviations (sd) are also shown.

Season	Habitat	N	$\delta^{15}\text{N}$	sd	$\delta^{13}\text{C}$	sd	$\delta^{34}\text{S}$	sd
Winter	Standing	19	-17.50	0.14	12.09	0.24	17.58	0.38
	Toppled	3	-17.22	0.13	12.21	0.41	17.28	0.05
Spring	Standing	14	-17.36	0.33	12.22	0.54	17.44	0.53
	Toppled	5	-17.33	0.19	12.18	0.33	17.71	0.46
Summer	Standing	7	-17.46	0.22	12.29	0.24	17.64	0.50
	Toppled	1	-17.54	.	12.50	.	17.87	.
Fall	Standing	3	-17.44	0.22	12.18	0.20	17.04	0.83
	Toppled	4	-17.31	0.12	12.37	0.20	17.27	0.41

Mean values of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ for rock sea bass (*Centropristis philadelphica*) collected over two habitat types in the Gulf of Mexico, including standing oil and gas platforms (standing) and toppled oil and gas platforms (toppled) habitat, by distance from the structure, combined over seasons and years. Total number of samples run (n) and standard deviations (sd) are also shown. Only the closest (0.25 km) and farthest (1.5 km) distances were run due to time and budget constraints.

Distance	Habitat	N	$\delta^{15}\text{N}$	sd	$\delta^{13}\text{C}$	sd	$\delta^{34}\text{S}$	sd
0.25 km	Standing	23	12.21	0.42	-17.43	0.28	17.46	0.55
	Toppled	9	12.29	0.27	-17.27	0.15	17.43	0.39
1.5 km	Standing	20	12.13	0.28	-17.47	0.16	17.56	0.42
	Toppled	4	12.23	0.38	-17.41	0.15	17.62	0.51

VITA

Kirsten Ann Simonsen was born in November 1979, in Washington, D.C. She grew up in West Islip, New York, on the south shore of Long Island where she spent most of her time at the beach, looking for critters. It was here that she developed a love and curiosity about the marine environment. She graduated from West Islip Senior High School in 1997, and afterwards attended Roger Williams University in Bristol, Rhode Island, graduating *cum laude* with a Bachelor of Science in marine biology in 2001. After graduation, Kirsten worked for the Chesapeake Biological Laboratory in Solomons, Maryland as a research assistant in the Environmental Chemistry Department. However, she missed the marine world and its critters, and so in the fall of 2004, Kirsten entered the masters program in the Department of Oceanography and Coastal Sciences at Louisiana State University in the Fisheries Biology Laboratory, earning a M.S. under the supervision of Dr. James H. Cowan Jr. in May of 2008. She then accepted a position in the doctoral program in the Department of Oceanography and Coastal Sciences at Louisiana State University to continue working with Dr. James H. Cowan Jr., and will receive her PhD in May 2013. After graduation, Kirsten will move to Seattle, WA, where she has accepted an NRC Post-Doctorate at the National Marine Fisheries Service Alaska Fisheries Science Center, where will be ping the water column, continuing the search for critters in the Gulf of Alaska under the guidance of Dr. Patrick Ressler.